Interactions between habitat fragmentation and invasions: factors driving exotic plant invasions in native forest remnants, West Coast, New Zealand

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Abstract

Habitat fragmentation and biological invasions are widely considered to be the most significant threats to global biodiversity, and synergistic interactions between these processes have the potential to cause even greater biodiversity loss than either acting alone. The objective of my study was to investigate the effects of fragmentation on plant communities in native forest fragments, and to examine potential interactions between these effects and invasions by exotic plants at multiple spatial scales. I examined edge, area and landscape effects on plant invasions using empirical data from fragmented landscapes on the West Coast of New Zealand. My research revealed significant interactions between the amount of native forest cover in the landscape and the strength of edge and area effects on plant communities in forest fragments. The dominance of exotic plants in the community was highest at forest edges and decreased towards fragment interiors, however the interiors of very small fragments were relatively more invaded by exotic plants than those in larger fragments, reflecting a significant interaction between edge and area effects. Similarly, exotic dominance increased in more heavily deforested landscapes, but this effect was only apparent in very small fragments (<2 ha). The combined effects of small fragment size and low forest cover in the landscape appear to have promoted invasions of exotic plants in very small remnants.

I explored the mechanisms underlying edge-mediated invasions in forest fragments and examined whether propagule availability and/or habitat suitability may be limiting invasions into fragments. Experimental addition of exotic plant propagules revealed that landscape forest cover interacted with edge effects on germination, growth and flowering rates of two short-lived, herbaceous species, and this appeared to be driven by elevated light and soil phosphorus levels at edges in heavily deforested landscapes.

I also examined the role of traits in influencing plant responses to forest fragmentation. Different traits were associated with exotic invasiveness in edge and interior habitats of forest fragments, indicating that the traits promoting invasiveness were context dependent. Traits also had a major influence on responses of native plants to forest fragmentation, with generalist species appearing to benefit from fragmentation, as they can utilise both forest and open habitats, whereas native forest specialists have been negatively impacted by fragmentation.

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I declare that the material in this thesis is my own work, except for the following assistance: (1) Alison Botha, Josh Brown, Felix Collins, Raphael Didham, Juliane Geyer, Katie Grinstead, Keir Morse, Helge Pfingst, Katherine Speed, Jon Sullivan, Vanessa Westcott, Luke Worsham, and Juzah Zammit-Ross assisted with field data collection and experiments, (2) Claire Galilee, Dave Conder, Helge Pfingst, and Keir Morse assisted with the lab germination experiments, (3) Claire Galilee assisted with sieving and grinding soil samples (4) Phil Knightbridge and Peter Johnson assisted with identification of plant specimens, (5) Robert Ewers and Raphael Didham developed the edge gradient slope-fitting program in R which I used in Chapter 2, and (6) Raphael Didham designed the composite ANOVA method used to analyse the experimental data in Chapter 4. The entire thesis was written by myself, but received critical review by my supervisors Raphael Didham and Jon Sullivan.

Chapter 1 – The effects of habitat fragmentation and biological invasions on biodiversity

1.1 BACKGROUND TO RESEARCH

Habitat fragmentation and biological invasions are widely considered to be the most significant threats to global biodiversity, and have both been the subject of a vast amount of research and discussion (Vitousek *et al.* 1997; Wilcove *et al.* 1998; Mack *et al.* 2000; Fahrig 2003). More recently it has been recognised that synergistic interactions between fragmentation and invasions have the potential to cause even greater biodiversity loss than either acting alone (Hobbs 2001; Didham *et al.* 2007; Ricciardi 2007). Despite this significance, there has been very little integration between these processes in the conservation biology or ecology literature, with surprisingly little theoretical or empirical work on the effects of habitat fragmentation on invasive spread (With 2002; Didham *et al.* 2007). We do not know at what critical level of fragmentation invasive spread is most likely to occur, which stages of the invasion process might be enhanced by fragmentation, how the spatiotemporal dynamics of disturbance affect the invasibility of communities, or to what extent landscapes can be managed or restored to control invasive spread (With 2002). Nevertheless, understanding the effects of fragmentation on invasion processes could be essential for predicting and managing the spread of invasive species in fragmented landscapes (With 2002). In this chapter, I will briefly review the effects of fragmentation and invasions on biodiversity and the major theories relating to each process, as well as potential interactions between them.

1.1.1 Effects of habitat fragmentation on biodiversity

Habitat loss and fragmentation are major causes of global biodiversity loss, as they frequently result in reductions in population sizes leading to extinction (Turner 1996; Fahrig 2003). Fragmentation is usually defined as a landscape-scale process involving both habitat loss and the breaking apart of habitat (Fahrig 2003). In the strictest sense, fragmentation refers to the breaking apart of habitat independent of habitat loss (Fahrig 2003), however fragmentation occurs as a consequence of habitat loss, therefore the two processes are intricately linked (Laurance 2008). In this thesis, I define fragmentation as "the process whereby habitat loss results in the division of large, continuous habitats into smaller, isolated habitat fragments" (Ewers & Didham 2006a). The effects of fragmentation on biodiversity operate at multiple spatial scales, ranging from local (at

different distances from the edge within fragments), to patch (whole fragments), to landscape and regional scales (Collinge 1996). These effects can be examined separately, but they are not truly independent because the patterns and processes of fragmentation are usually inter-correlated and interact with each other (Ewers & Didham 2007).

Edge effects

Fragmentation creates abrupt changes in habitat or vegetation type with the resulting edge acting as a transition zone between the fragment and surrounding matrix habitats (Cadenasso *et al.* 2003). Forest fragmentation results in changes in environmental conditions at forest edges (abiotic effects), changes in species composition (direct biotic effects), and alteration of species interactions (indirect biotic effects); these are collectively referred to as "edge effects" (Saunders *et al.* 1991; Murcia 1995; Fagan *et al.* 1999). Abiotic effects at forest edges include increased radiation levels, air and soil temperatures, vapour pressure deficits, and wind speeds (Saunders *et al.* 1991; Matlack 1993; Young & Mitchell 1994; Chen *et al.* 1995; Murcia 1995; Chen *et al.* 1999; Didham & Lawton 1999; Davies-Colley *et al.* 2000; Gehlhausen *et al.* 2000; Laurance & Curran 2008). Concentrations of nutrients and pollutants may also be elevated at edges, as a result of human activities in the adjacent matrix (Weathers *et al.* 2001). Edge effects on microclimate tend to vary according to adjacent vegetation type and aspect, with the strongest effects occurring next to open habitats (Mesquita *et al.* 1999; Gehlhausen *et al.* 2000; Harper *et al.* 2005; Denyer *et al.* 2006) and at sunny, north-facing edges in the southern hemisphere (or south-facing edges in the northern hemisphere) (Brothers & Spingarn 1992; Matlack 1993; Fraver 1994; Young & Mitchell 1994; Gehlhausen *et al.* 2000).

Changes in plant communities frequently occur at edges in response to these abiotic effects, and include changes in species composition and seedling recruitment patterns, lower tree basal areas, and elevated canopy tree mortality (Lovejoy *et al.* 1986; Williams-Linera 1990; Brothers & Spingarn 1992; Chen *et al.* 1992; Fox *et al.* 1997; Laurance *et al.* 1998a; Laurance *et al.* 1998b; Fagan *et al.* 1999; Mesquita *et al.* 1999; Sizer & Tanner 1999; Laurance *et al.* 2001; Bruna 2002; Benítez-Malvido & Martínez-Ramos 2003; Bach *et al.* 2005; Harper *et al.* 2005; Laurance *et al.* 2006; Marchand & Houle 2006). Although the majority of forest-dwelling species are likely to be negatively affected by forest fragmentation, some species appear to be unaffected or respond positively to edge and area effects (Grashof-Bokdam 1997; Bender *et al.* 1998; Harper & MacDonald 2001; Laurance *et al.* 2002). For example, large, old-growth trees may be replaced by

shorter-lived successional trees (Laurance *et al.* 2006), and the density of lianes may increase near edges (Laurance *et al.* 2001).

Changes in the abundance and diversity of birds (Hagan *et al.* 1996; Hawrot & Niemi 1996), mammals (Oehler & Litvaitis 1996; Pasitschniak-Arts & Messier 1998), lizards (Anderson & Burgin 2002), and insects (Margules *et al.* 1994; Didham *et al.* 1998; Foggo *et al.* 2001; Ewers & Didham 2008) at edges have also been reported. Altered species interactions at edges include predation (Donovan *et al.* 1997; Winter *et al.* 2000; Lahti 2001; Meiners & LoGiudice 2003), competition (Remer & Heard 1998), herbivory (Cadenasso & Pickett 2000), and pollination (Hobbs & Yates 2003; Montgomery *et al.* 2003), and seed dispersal (Kollmann & Schneider 1999; Hobbs & Yates 2003). For example, in Amazonia lush plant growth along newly created edges resulted in an increase in insect herbivores which in turn attracted insectivorous species, altering the species composition of rainforest fragments relative to contiguous forest (Lovejoy *et al.* 1989). Increased rates of species turnover or hyperdynamism in population and community dynamics can also occur at edges (Didham *et al.* 1998; Laurance 2002). Flower production and pollination rates may increase at forest edges in some plant species but decrease in others, and this will have a major effect on fruit and seed set, and ultimately population viability (Jules & Rathcke 1999; Kollmann & Schneider 1999; Cunningham 2000; Hobbs & Yates 2003; Montgomery *et al.* 2003; Honnay *et al.* 2005).

Most empirical studies have found that edge effects penetrate less than 150 metres into fragmented forests (Matlack 1993; Malcolm 1994; Young & Mitchell 1994; Fox *et al.* 1997; Didham & Lawton 1999; Mesquita *et al.* 1999; Sizer & Tanner 1999; Harper & MacDonald 2002; Norton 2002; Harper *et al.* 2005; Broadbent *et al.* 2008), although a few studies have reported much greater distances (Laurance 1991; Curran *et al.* 1999; Laurance 2000; MacQuarrie & Lacroix 2003; Ewers & Didham 2008). For example, increased disturbance levels and exotic plants were detected up to 500 metres from edges in Australian tropical forest fragments (Laurance 1991). The physical structure of an edge can have a major influence on the strength of edge effects in fragments, as edges mediate many of the interactions between the patch and the matrix (Camargo & Kapos 1995; Didham & Lawton 1999; Cadenasso & Pickett 2001; Weathers *et al.* 2001; Harper *et al.* 2005). Following edge creation, plants may alter their growth habit and create a ‘curtain’ of dense vegetation formed from lateral branches of trees and shrubs, which can impede the flow of organisms and materials into fragments (Camargo & Kapos 1995; Cadenasso & Pickett 2001; Marchand & Houle 2006). The age of an edge will also influence the strength of edge effects, as forest plants may take a number of years to respond to edge creation (Brothers &

Spingarn 1992; Matlack 1994b; Harper & MacDonald 2002). Newly created forest edges (often referred to as 'hard edges') are usually more open and permeable than older edges, which may become buffered by dense vegetation over time (i.e. 'soft edges') (Didham & Lawton 1999; Cadenasso & Pickett 2001).

Area effects

Forest fragmentation results in a reduction in the area of habitat available for forest-dwelling species, and separation of formerly continuous habitat into discrete fragments leading to increased isolation of fragments (Simberloff & Abele 1982). Island biogeography theory has been applied to habitat fragmentation, and as in true islands, a positive relationship between fragment area and species richness is predicted (MacArthur & Wilson 1967; Simberloff & Abele 1982; Hanski & Gilpin 1991). Consequently, local extinction rates are predicted to increase following fragmentation as insular biotas 'relax' to a lower equilibrium species number (MacArthur & Wilson 1967; Connor & McCoy 1979; Tilman *et al.* 1994; Newmark 1996; Turner 1996). There are a number of explanations for this relationship, including (1) larger fragments have greater habitat heterogeneity which facilitates the existence of ecological specialists and greater diversity of species, (2) larger areas support larger populations of species which have a lower probability of extinction, (3) the probability of immigration is higher for larger fragments as they are a larger target for dispersing species (MacArthur & Wilson 1967; Connor & McCoy 1979; Hanski & Gyllenburg 1997), and (4) speciation rates may be higher in larger areas (Losos & Schluter 2000). Fragment isolation is expected to reduce population sizes and increase extinction rates because the probability of immigration into fragments is lower, and therefore so is the chance of declining populations being rescued (Hanski & Gilpin 1991; Collinge 1996; Hanski 1998; Fahrig 2003; Piessens *et al.* 2005). Individuals in small populations may also have lower reproductive output, leading to further population decline (Young *et al.* 1996; Jacquemyn *et al.* 2002; Honnay *et al.* 2005).

Although many studies have reported a positive species-area relationship in fragments; for example in plants (Peterken & Game 1984; Grashof-Bokdam 1997; Honnay *et al.* 1999; Hill & Curran 2001; Benítez-Malvido & Martínez-Ramos 2003; Petit *et al.* 2004), birds (Cornelius *et al.* 2000; Watson *et al.* 2005), mammals (Dunstan & Fox 1996; Newmark 1996), and insects (Kruess & Tscharntke 2000; Krauss *et al.* 2003; Steffan-Dewenter 2003; Vasconcelos *et al.* 2006); others have found a weak or no relationship between area and species richness (Kelly *et al.* 1989; Pärtel & Zobel 1999; Krauss *et al.* 2004; Helm *et al.* 2006). One explanation for this is that populations

of long-lived species, such as trees, could take decades or even centuries to respond to reduced habitat area – a situation referred to as the "extinction debt" (Tilman *et al.* 1994; Brooks *et al.* 1999; Hanski & Ovaskainen 2002). In this case, species may persist in suboptimal habitats for some time, and species diversity may be more closely related to historical habitat cover than current land cover patterns (Lindborg & Eriksson 2004; Snall *et al.* 2004; Honnay *et al.* 2005; Helm *et al.* 2006). Another explanation is that species turnover may increase following fragmentation, leading to altered species composition in fragments, while species richness remains relatively unchanged (Leigh *et al.* 1993; Laurance 2002; Sodhi *et al.* 2005).

In addition to these 'biogeographic' effects, the size of a fragment is important because it determines the amount of interior or core habitat that is not influenced by edge effects (Janzen 1983; Laurance & Yensen 1991; Murcia 1995). Larger fragments have a larger core area, which is critical for species that can only persist in interior habitats (Janzen 1983). Fragment shape also influences the area of habitat exposed to edge effects, as long thin fragments have less core area than circular fragments of the same total area (Laurance & Yensen 1991; Collinge 1996; Yamaura *et al.* 2008). Because of their increased exposure to edge effects and accessibility to humans, small fragments are likely to experience elevated levels of disturbance, which can lead to changes in plant species composition, stand structure, regeneration cycles, and animal communities (Janzen 1983; Hobbs & Huenneke 1992; Dunstan & Fox 1996; Laurance *et al.* 1998a; Hobbs 2001; Echeverría *et al.* 2007). Types of disturbance include major fluxes in water and solar radiation, fire, wind-throw, grazing by domestic and wild animals, logging, drainage, irrigation, and nutrient enrichment (Saunders *et al.* 1991; Hobbs & Huenneke 1992; Hobbs 1993; Kemper *et al.* 1999; Gascon *et al.* 2000; Cochrane 2001; Laurance 2004; Duncan *et al.* 2008; Laurance & Curran 2008). Small fragments are usually more accessible to domestic stock, and hence are subject to higher grazing pressure and nutrient enrichment by animal faeces and urine (Duncan *et al.* 2008). Grazing can have major effects on plant species composition, as some species are more vulnerable than others because of their palatability and growth form (Yates *et al.* 2000; Kirby 2001; Smale *et al.* 2005). A study in southern Chile confirmed that small fragments were more disturbed than large patches, with more tree stumps, animal trails and cow pats (Echeverría *et al.* 2007). Tree basal area and canopy cover declined with decreasing patch size, implying that fragmentation had caused mortality of large trees, and may be affecting successional processes in forest fragments (Echeverría *et al.* 2007). Small fragments are also more vulnerable to the influx of agricultural chemicals such as pesticides, herbicides and fertilizers from surrounding farmland (Weathers *et al.* 2001; Stevenson 2004; Duncan *et al.* 2008).

Effects of landscape context

Characteristics of the surrounding landscape matrix and the spatial arrangement of fragments (referred to as 'landscape structure' or 'landscape context') can have major effects on species and processes occurring in fragments (Fahrig & Merriam 1994; Collinge 1996; Davies *et al.* 2001; Murphy & Lovett-Doust 2004), particularly if external disturbances such as grazing or fire act synergistically with the effects of fragmentation (Cochrane 2001; Hobbs 2001). Landscape context is therefore considered to be of central importance in understanding the effects of fragmentation on population and community dynamics (Fahrig & Merriam 1994; de Blois *et al.* 2002). The development of landscape ecology as a discipline led to a significant shift in the focus of conservation biology from single species to higher levels of organisation such as ecosystems and landscapes, and a greater understanding of patterns and processes at larger scales (Hobbs 1994). Landscape ecology is essentially the study of how spatial pattern (i.e. landscape structure) affects ecological processes (Turner 1989; Pickett & Cadenasso 1995). It includes elements of classical island biogeography theory such as the species-area relationship, as well as theory about metapopulation dynamics and fragmentation, which are important for understanding the effects of fragmentation on species diversity (Collinge 1996). It also recognises that landscapes are heterogeneous and that species in fragments interact with the surrounding matrix, which may have varying degrees of habitat suitability (Murphy & Lovett-Doust 2004; Kupfer *et al.* 2006). For example, the presence of secondary vegetation in the matrix may reduce the impacts of fragmentation on forest-dwelling species, if they are able to make use of it (Mesquita *et al.* 1999; Ricketts 2001; Debinski 2006; Ewers & Didham 2006a; Kupfer *et al.* 2006; Vasconcelos *et al.* 2006).

Deforested landscapes are highly modified and are usually much more dynamic than landscapes with intact forest (Saunders *et al.* 1991; McIntyre & Hobbs 1999; Laurance & Cochrane 2001; Laurance 2002; Fischer & Lindenmayer 2007; Laurance 2008). These modified landscapes are likely to experience ongoing changes in human activity and land use (Laurance & Cochrane 2001), and a higher intensity of disturbances such as grazing (Yates *et al.* 2000), logging (Echeverría *et al.* 2007), fires (Cochrane 2001), irrigation or drainage of soils (Hobbs 1993), and pollution from agricultural pesticides, herbicides and fertilizers (Duncan *et al.* 2008). Deforestation also leads to increasing wind speeds, which cause increased wind-throw and damage to trees in forest fragments, particularly at edges (Hobbs 1993; Laurance 2004; Laurance & Curran 2008).

Fragmentation creates barriers to dispersal as some species are unable or reluctant to move across matrix habitats between fragments (Debinski & Holt 2000). This in turn affects metapopulation persistence, as some species may be unable to recolonise patches where populations have become locally extinct (Dias 1996; Murphy & Lovett-Doust 2004). The extent to which a matrix impedes movement depends on its characteristics and spatial configuration (Fahrig & Merriam 1994; Kupfer *et al.* 2006), which is perceived at different spatial scales by individual species (Kotliar & Wiens 1990; Roland & Taylor 1997; St. Clair *et al.* 1998; Chust *et al.* 2004). For example, Kruess & Tscharntke (2000) found that parasitoids and herbivores responded differently to spatial scale in fragmented old meadows, with parasitoids being more sensitive to habitat loss and isolation than their phytophagous hosts. The ability of species to use matrix habitats is likely to affect their vulnerability to extinction in fragmented landscapes (Andrén 1997; Gascon *et al.* 1999; Murphy & Lovett-Doust 2004; Kupfer *et al.* 2006). In central Amazonia, Gascon *et al.* (1999) studied the responses of four animal groups to forest fragmentation and found that three groups (birds, small mammals and frogs) had significant negative correlations between their abundance in the matrix and vulnerability to local extinction. This suggests that species that avoid matrix habitats tend to decline or disappear in fragments, while those that tolerate or exploit the matrix often remain stable or increase.

Interactions with pollinators and dispersers can have a major influence on plant population dynamics in fragmented landscapes (Kremen & Ricketts 2000; Lennartsson 2002; Hobbs & Yates 2003). Populations of avian pollinators and dispersers may be reduced as a result of habitat loss and fragmentation, leading to a breakdown in plant-animal mutualisms, and a decline in plant reproductive success (van Ruremonde & Kalkhoven 1991; Cordeiro & Howe 2001; Lennartsson 2002). A study by Díaz *et al.* (2005) found that the density of bird species associated with old-growth forests in central Chile was reduced in young forest fragments compared to late successional forests, and suggested this was due to changes in the availability of canopy emergent trees. In New Zealand, there is concern that the decline of the native wood pigeon or kereru *(Hemiphaga novaeseelandiae)*, caused by a combination of habitat loss and predation, may have serious consequences for the long-term survival of large-fruited native trees, as it may be the only species capable of ingesting and dispersing their fruit (Clout & Hay 1989).

The amount of habitat in a landscape is likely to have a major influence on metapopulation persistence, with the probability of persistence increasing with greater habitat cover because of the increased likelihood of dispersal between sub-populations in fragments (Hanski & Ovaskainen 2000; Fahrig 2003). However, this may not be a linear relationship (as predicted by the

'proportional area hypothesis') (Fahrig 2003), and a number of theoretical studies have suggested that there may be a threshold for population persistence at 10-30% habitat cover in the landscape (referred to as the 'extinction threshold hypothesis') (Andrén 1994, 1997; Fahrig 1998, 2002; Lennartsson 2002; Huggett 2005). Below this 'landscape threshold', connectivity between remaining fragments decreases abruptly and the effects of fragmentation become disproportionately more severe, with disruption of dispersal, species interactions, and edge-mediated processes, leading to a sharp decline in metapopulation survival (With 1997; Fahrig 1998; With & King 1999). This suggests that in landscapes with a high proportion of forest remaining, forest loss alone will drive population dynamics, whereas below the critical threshold, fragmentation effects could have a greater influence on metapopulation survival than forest loss alone (Andrén 1994, 1997). A number of empirical studies have supported this hypothesis (Jansson & Angelstam 1999; Villard *et al.* 1999; Collingham & Huntley 2000; Radford & Bennett 2004; Dodd *et al.* 2006; Betts *et al.* 2007; Frair *et al.* 2008), however other studies have found no evidence for landscape thresholds (Lindenmayer *et al.* 1999; Parker & Mac Nally 2002; Lindenmayer *et al.* 2005), and the concept has yet to be adequately tested (Huggett 2005; Lindenmayer & Luck 2005).

Interactions between edge, area and landscape effects

Fragmentation effects occurring at multiple spatial scales – edge, patch and landscape – may interact with each other in complex ways. Interactions between edge and area effects have been reported for insects and plants in forest fragments, with edge gradients often being more severe in small fragments (Malcolm 1994; Didham *et al.* 1998; Barbosa & Marquet 2002; Ewers *et al.* 2007). For example, a study in the central Amazon revealed that edge effects on forest vegetation structure were strongest in small fragments (Malcolm 1994). The most likely explanation appears to be that small fragments have a higher density of edge per unit area than large fragments, hence they are exposed to the effects of multiple edges (Laurance & Yensen 1991; Malcolm 1994). Interactions between landscape cover and edge effects have also been documented, as a number of studies have found that landscape context can influence patch-scale predation by invasive species (Robinson *et al.* 1995b; Donovan *et al.* 1997; Hartley & Hunter 1998; Lahti 2001). For example, in the American Midwest, nest predation rates by cowbirds were higher at edges than fragment interiors, but only in moderately to highly fragmented landscapes (Donovan *et al.* 1997). More complex interactions between edge, area and landscape effects could also occur in fragmented habitats, however, to my knowledge the importance of multiple interactions between fragmentation effects has never been investigated in one study.

1.1.2 Biological invasions

Biological invasions are considered to be the second largest threat to global biodiversity, after habitat destruction (Vitousek *et al.* 1997; Mack *et al.* 2000), and are one of the potential synergistic drivers of species loss in fragmented landscapes (Didham *et al.* 2007; Ricciardi 2007). Increased global trade and human transportation has been accompanied by the spread of species around the world, either deliberately or accidentally, due to the breakdown of geographic barriers (Baskin 1998; Mack & Lonsdale 2001; D'Antonio & Kark 2002; Ehrenfeld 2005). At the same time, human activities have modified the global environment in ways that enhance the establishment of invasive species (Dukes & Mooney 1999; Henderson *et al.* 2006). The spread of invasive species, and resulting 'biotic homogenization', is considered to be a major driver of global environmental change which could have potentially serious consequences for human welfare (Vitousek *et al.* 1997; McKinney & Lockwood 1999; Chapin *et al.* 2000; Mack *et al.* 2000; Rosenzweig 2001; Olden 2006; Ricciardi 2007; Tylianakis *et al.* 2008).

Invasive plants have a number of impacts on biodiversity, and these vary according to the interactions between the invader, the physical environment, and characteristics of the recipient community (Parker *et al.* 1999; Mack *et al.* 2000; D'Antonio & Kark 2002; Henderson *et al.* 2006). Invasive plants threaten the long-term survival of native communities by displacing native species, altering successional processes, disrupting plant reproductive mutualisms, reducing and fragmenting native plant populations, and hybridising with native plant species (Vitousek & Walker 1989; Richardson 1998; Standish *et al.* 2001; D'Antonio & Kark 2002; Williams *et al.* 2003; D'Antonio & Hobbie 2005; Yurkonis *et al.* 2005; Henderson *et al.* 2006; Traveset & Richardson 2006). Invasive plants can have wide-ranging impacts on ecosystem processes and disturb the flow of energy and nutrients through ecosystems by altering nutrient cycling, decomposition rates, and moisture levels (Vitousek *et al.* 1987; Ehrenfeld *et al.* 2001; Levine *et al.* 2003; Standish *et al.* 2004; D'Antonio & Hobbie 2005). They can also change the frequency and intensity of disturbances to ecosystems, which may result in the maintenance of ecosystems in a new or transitional state (Mack & D'Antonio 1998). Once established, invasive species may also facilitate the invasion of other exotic species by increasing their likelihood of survival and/or magnitude of impact, thus potentially leading to an 'invasional meltdown' (Simberloff & von Holle 1999; Bourgeois *et al.* 2005).

A wide range of terms have been applied to non-native plants in the invasion biology literature, however inconsistent terminology may impede progress in research (Henderson *et al.* 2006),

therefore consistent definitions are essential (Richardson *et al.* 2000b). In this thesis, I will apply the definitions given by Richardson *et al.* (2000b): *'Exotic'* (also referred to as 'introduced', 'alien' or 'non-native') species are those that have been introduced by humans, either deliberately or accidentally, into an area outside their natural range. *'Naturalised'* species are exotic plants "that reproduce consistently and sustain populations over many life cycles without direct intervention by humans." *'Invasive'* species are "naturalised plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants…and have the potential to spread over a considerable area." *'Weeds'* are "plants that grow in sites where they are not wanted and which usually have detectable economic or environmental effects."

Biological invasions involve several key stages: dispersal, establishment, population increase, and geographical spread (Shea & Chesson 2002; With 2002; Dietz & Edwards 2006; Henderson *et al.* 2006). Each stage is affected by different factors operating across a range of spatial and temporal scales (Pauchard & Shea 2006; Gravuer *et al.* 2008). Propagule pressure (or introduction effort) is a major factor during the invasion process because the chance of successful establishment increases with the rate of arrival at a potential invasion site (Williamson & Fitter 1996a; Kolar & Lodge 2001; Duncan *et al.* 2003; Leung *et al.* 2004; von Holle & Simberloff 2005; Richardson & Pysek 2008). The dispersal of propagules is also a crucial stage, as dispersal barriers must be overcome in order for invasion to occur (Puth & Post 2005; von der Lippe & Kowarik 2007). Following dispersal, the establishment and growth of a plant species depend on the opportunities and resources that the invaded community provides for the invader (Shea & Chesson 2002). For example, many invasive plants are light-demanding and require elevated light levels for successful germination and growth (Kelly & Skipworth 1984; Brothers & Spingarn 1992; Duggin & Gentle 1998; Meekins & McCarthy 2001; Charbonneau & Fahrig 2004). Environmental conditions must also be suitable for successful reproduction, including the presence of pollinators and dispersers, in order for further spread to occur (Richardson *et al.* 2000a).

Much research and discussion has focused on understanding why certain species become pests and predicting future invasions and their impacts (Noble 1989; Pimm 1989; Rejmánek & Richardson 1996; Williamson 1996; Williamson & Fitter 1996b; Goodwin *et al.* 1999; Lonsdale 1999; Williamson 1999; Kolar & Lodge 2001; D'Antonio & Kark 2002; Heger & Trepl 2003; Levine *et al.* 2003; Hamilton *et al.* 2005; Melbourne *et al.* 2007; Kilroy *et al.* 2008). Despite these efforts, there is still a lack of general theory regarding the traits of invaders and invasibility (Lonsdale 1999; Parker *et al.* 1999; Sax *et al.* 2005), and a key challenge in invasion biology is to understand the interactions of species traits and ecosystem properties in determining which

species will become invasive and where (D'Antonio & Kark 2002; Heger & Trepl 2003). Development of robust invasion biology theory will provide crucial information for better management of invasive species and allow restoration ecologists to design communities that will better resist invasions (Seabloom *et al.* 2003).

Invasiveness and species traits

Many authors have attempted to define a suite of traits to predict which species will become invasive, and a number of characteristics of successful plant invaders have been proposed (Baker 1965; Amor & Piggin 1977; Noble 1989; Roy 1990; Rejmanek 1996; Rejmánek & Richardson 1996; Daehler 1998; Bellingham *et al.* 2004; Hamilton *et al.* 2005; Thuiller *et al.* 2006; Thompson & McCarthy 2008). These include: short juvenile period, rapid growth, long flowering period, high seed output, vegetative reproduction, long-distance dispersal, and human commensalism (Baker 1965; Amor & Piggin 1977; Roy 1990; Rejmanek 1996; Rejmánek & Richardson 1996; Williamson & Fitter 1996b; Daehler 1998; McKinney & Lockwood 1999). Despite the appeal of developing a suite of traits to predict invasiveness, however, the definition of an ideal invader has proven to be problematic, as few invading species possess all of these characteristics (Alpert *et al.* 2000; Thompson *et al.* 2001; Heger & Trepl 2003; Moles *et al.* 2008; Whitney & Gabler 2008). The importance of particular traits in contributing to invasion success is inevitably context dependent and will depend on the habitat or community encountered, or the stage of invasion (Thompson *et al.* 1997; Alpert *et al.* 2000; Kolar & Lodge 2001; Heger & Trepl 2003; Lake & Leishman 2004; Lloret *et al.* 2005; Facon *et al.* 2006; Richardson & Pysek 2006; Milbau & Stout 2008).

Invasibility

The invasibility of a community (susceptibility to invasion) is affected by a variety of factors, including environmental characteristics (e.g. soil fertility, light level, presence of bare soil, degree of environmental stress), the density of individuals (e.g. crowding effects, thickness of forest edge vegetation), and species diversity, which affects the complexity of the food web and strength of community interactions (Fox & Fox 1986; Rejmánek 1989; Levine & D'Antonio 1999; Alpert *et al.* 2000; Milbau & Nijs 2004; Henderson *et al.* 2006). The diversity-resistance hypothesis predicts that species-poor communities will be more readily invaded because vacant niches exist and interspecific competition is low meaning resident species may be easily displaced by invaders (Elton 1958; Kennedy *et al.* 2002). Many studies have provided support for this hypothesis and

found a negative relationship between native species diversity and the diversity of invaders (McIntyre & Lavorel 1994; Tilman 1997; Stachowicz *et al.* 1999; Naeem *et al.* 2000; Dukes 2001; Kennedy *et al.* 2002; King & Buckney 2002; Brown & Peet 2003; Milbau & Nijs 2004). For example, King & Buckney (2002) found that the number of native plant species was negatively correlated with the percentage and number of exotic species in urban bushland sites in Sydney. However, other studies have found no relationship or the opposite trend – a positive relationship between the diversity of native and exotic species (Robinson *et al.* 1995a; Planty-Tabacchi *et al.* 1996; Wiser *et al.* 1998; Levine & D'Antonio 1999; Lonsdale 1999; Stohlgren *et al.* 1999; Levine 2000; Fornwalt *et al.* 2003; Keeley *et al.* 2003; Bruno *et al.* 2004; Houlahan & Findlay 2004; Howard *et al.* 2004; Meiners *et al.* 2004).

One reason that these conflicting results may occur is because the influence of species richness on invasibility may be confounded with other underlying factors driving invasions and species diversity, such as disturbance regime or soil fertility (Levine & D'Antonio 1999; Prieur-Richard & Lavorel 2000; Davis *et al.* 2005). Another explanation is that different processes may be occurring at different spatial scales, hence the results will be influenced by the scale of each study (Shea & Chesson 2002; Brown & Peet 2003; Byers & Noonburg 2003; Knight & Reich 2005; Pauchard & Shea 2006). At a local scale, community structure may be strongly affected by competitive interactions between species, whereas at larger scales native and exotic species may respond in a similar way to varying environmental conditions such as nutrient status or temperature (referred to as the 'extrinsic covariance hypothesis') (Levine & D'Antonio 1999; Levine 2000; Kennedy *et al.* 2002; Shea & Chesson 2002; Stohlgren *et al.* 2002; Davis *et al.* 2005; Diez *et al.* 2008). Finally, species richness may not reflect the functional diversity of a community or ecosystem (as determined by the traits of resident species, number of trophic levels, and interspecific interactions), however functional diversity is likely to drive invasibility more than species richness *per se* because it determines the strength of competitive interactions and niche availability (Lavorel *et al.* 1999; Chapin *et al.* 2000; Prieur-Richard & Lavorel 2000; Dukes 2001).

Disturbance is widely acknowledged to be a key factor promoting plant invasions (Amor & Piggin 1977; Hobbs & Atkins 1988; Hobbs 1989; Hobbs & Huenneke 1992; Burke & Grime 1996; Lozon & MacIsaac 1997; Duggin & Gentle 1998; Fine 2002; Keeley *et al.* 2003). Disturbance increases community invasibility because it removes resident species, disrupts species interactions, and increases the amount of resources available (e.g. space, light, water, nutrients), thus reducing the effects of competition and creating opportunities which an exotic species may

be able to exploit (Sousa 1984; Fox & Fox 1986; Lewin 1987; Davis *et al.* 2000; Shea & Chesson 2002). In forest habitats, breaks in the forest canopy, through logging, wind damage or death of canopy trees, accompanied by disturbance of the ground cover (through uprooting of trees or animal browsing), result in increased forest floor irradiance and soil nitrogen levels, which can assist invasion by exotic plants (Maule *et al.* 1995). A review by Lozon & MacIsaac (1997) examined the role of disturbance in invasions in 63 field studies and revealed that grazing by domestic and wild animals was the most important factor associated with the establishment of exotic plants. Grazing can alter the composition of plant communities by reducing the aboveground biomass of palatable species, increasing nutrient availability through deposition of faeces and urine, and altering light and temperature regimes at the soil surface (Lozon & MacIsaac 1997; Hobbs 2001; Vavra *et al.* 2007). Grazing animals can also act as vectors for the introduction of exotic seeds, and cause disruption of the soil surface, which further assists the establishment of colonists (Vavra *et al.* 2007).

Interactions between invasiveness and invasibility

A number of authors have stressed the limitations of studying invasiveness and invasibility independently, and emphasised that interactions between invader attributes and those of the recipient community are critical for determining invasion success (Lodge 1993; Meiners *et al.* 2004; Milbau & Nijs 2004; Facon *et al.* 2006; Richardson & Pysek 2006). This approach has been referred to as a type of 'lock and key' model, where different traits favour invasiveness in different situations (Heger & Trepl 2003). For example, shade-tolerance will assist plant invasions in forest habitats where light availability is low (Martin & Marks 2006), whereas short germination time and rapid growth rate will facilitate invasion in grasslands (Milbau & Nijs 2004). A study on the traits of plant invaders in Europe found that clonal growth and competitive ability were important attributes in relatively undisturbed communities in cool, damp climates, whereas r-selected characteristics (such as high seed output) were associated with invasions in drier, open habitats (Thompson *et al.* 1997). The importance of particular traits may also change over time in response to temporal variability in the environment or invaded community (Davis *et al.* 2000; Thompson *et al.* 2001; Dietz & Edwards 2006; Richardson & Pysek 2006).

1.1.3 Interactions between habitat fragmentation and invasions

Habitat fragmentation and invasions are major drivers of biodiversity loss, and interactions between these processes could have major consequences for native communities in fragmented

landscapes (With 2002; Didham *et al.* 2007). Forest fragments are affected by a range of processes occurring in the surrounding landscape (Davies *et al.* 2001), and are increasingly exposed to the threat of invasive species (Vitousek *et al.* 1997). Fragmentation has been described as a "landscape-level" disturbance (Hobbs & Huenneke 1992), and since disturbance generally promotes invasion, fragmentation is expected to facilitate the establishment and spread of invasive species (With 2002). External disturbances in fragmented landscapes such as grazing or fire can act synergistically with the effects of fragmentation to promote invasion (Hobbs & Huenneke 1992; Cochrane 2001; Hobbs 2001). For example, research in Australia revealed that grazing in the adjacent landscape appeared to increase the invasion of exotic plants into woodland fragments (Yates *et al.* 2000; Hobbs 2001).

The interaction between invasive species and forest edges is an important part of the invasion process, as edges are often the first point of contact for fluxes of organisms and material from the surrounding landscape matrix, and tend to trap airborne particles and animal dispersers (Brothers & Spingarn 1992; Cadenasso & Pickett 2001; Weathers *et al.* 2001). Altered conditions at edges are likely to make forest fragments more vulnerable to invasion because they tend to favour the establishment and survival of exotic species (Ranney *et al.* 1981; Brothers & Spingarn 1992; Fox *et al.* 1997; Boutin & Jobin 1998; Yates *et al.* 2004). These changes include increased light, temperature and nutrient levels, reduced humidity, increased exposure to wind, grazing, and other disturbances (Saunders *et al.* 1991; Young & Mitchell 1994; Chen *et al.* 1995; Murcia 1995; Fox *et al.* 1997; Duggin & Gentle 1998; Weathers *et al.* 2001; Harper *et al.* 2005). Establishment of exotic plants at edges may lead to their penetration into fragment interiors over time (Fraver 1994), however the physical structure of an edge has an important influence on fragment invasibility, as edges with a dense 'curtain' of native shrubs and other vegetation can impede the flow of organisms into fragments (Didham & Lawton 1999; Cadenasso & Pickett 2001; Cadenasso *et al.* 2003).

Fragment size and shape influence fragment invasibility because they determine the amount of interior or core habitat that is not influenced by the edge (Janzen 1983; Laurance & Yensen 1991; Ewers & Didham 2006a). Small fragments are likely to be more susceptible to invasions because of their greater exposure to edge effects and higher levels of disturbance than in larger remnants (Janzen 1983; Kemper *et al.* 1999; Hobbs 2001; Stevenson 2004; Echeverría *et al.* 2007; Duncan *et al.* 2008). Long, thin fragments are likely to be more vulnerable to invasion because they have a greater length of edges and less core area than circular fragments of the same total area (Collinge 1996; Yates *et al.* 2004).

A number of recent studies have highlighted the important influence of landscape context on many aspects of the invasion process in fragmented landscapes, such as the propagule pressure and dispersal of invasive species, and the invasibility of fragments (With 2002; Pauchard & Alaback 2004; With 2004; Deckers *et al.* 2005; Bartuszevige *et al.* 2006; Buckley *et al.* 2006; Henderson *et al.* 2006; Duguay *et al.* 2007; Nesslage *et al.* 2007). Fragments in more heavily deforested landscapes are likely to be more heavily invaded by exotic plants because they are subject to greater exotic propagule pressure from the surrounding landscape (Boutin & Jobin 1998; Barlow & Kean 2004; Charbonneau & Fahrig 2004; With 2004; Duguay *et al.* 2007) and are more susceptible to invasion because they are more modified and disturbed than fragments in intact landscapes (Saunders *et al.* 1991; Hobbs 1993; McIntyre & Hobbs 1999; Hobbs 2000; With 2002; Fischer & Lindenmayer 2007).

Human activities will have a major influence on exotic propagule pressure, as increased human modification and disturbance in fragmented landscapes is likely to facilitate the establishment and spread of invasive species (Lozon & MacIsaac 1997; Burke & Nol 1998; With 2004; Alston & Richardson 2006; Guirado *et al.* 2007; von Holle & Motzkin 2007). In fragmented landscapes, matrix vegetation is usually dominated by exotic species, many of which are deliberately propagated by humans for a variety of uses, such as high-producing pasture, fodder crops, shelterbelts, timber, horticulture and ornamental (Cadotte & Lovett-Doust 2001; Dehnen-Schmutz *et al.* 2007b; Duguay *et al.* 2007). Many studies conducted over a broad range of spatial scales and regions have shown that the abundance and diversity of exotic plants tends to increase with human population density and infrastructure such as roads (Timmins & Williams 1991; Tyser & Worley 1992; Lozon & MacIsaac 1997; Vilà & Pujadas 2001; Pyšek *et al.* 2002; Aragón & Morales 2003; Gelbard & Belnap 2003; Watkins *et al.* 2003; Lundgren *et al.* 2004; Sullivan *et al.* 2004; Bartuszevige *et al.* 2006; Sanz-Elorza *et al.* 2006; Duguay *et al.* 2007; Guirado *et al.* 2007). For example, Sullivan *et al.* (2005) recorded higher numbers of exotic plant species in native forest remnants adjacent to more densely populated areas in Northland, New Zealand.

Interactions with animal pollinators and dispersers play a key role in the spread of invasive plants in fragmented landscapes (With 2002; Buckley *et al.* 2006). Populations of exotic animals are likely to be higher in more heavily deforested landscapes, as these modified habitats are usually more suitable for them and hence support higher population densities than intact forest (With 2002; Buckley *et al.* 2006). In general, exotic frugivores tend to preferentially consume exotic plants, therefore larger populations of exotic frugivores are likely to promote higher rates of

dispersal and recruitment of fleshy-fruited exotic plants (Williams & Karl 1996; Bourgeois *et al.* 2005). Native frugivores may also consume exotic plants if these are abundant in the landscape (Cordeiro *et al.* 2004; Buckley *et al.* 2006). Landscape cover will also influence movement patterns and behaviour of animal mutualists, which in turn affect the reproduction and dispersal of invasive plants (van Ruremonde & Kalkhoven 1991; Hutchinson & Vankat 1997b; Kollmann & Schneider 1999; Gosper *et al.* 2005; Buckley *et al.* 2006). Forest fragments may attract vertebrate seed dispersers and act as recruitment foci for exotic plants because dispersers use them as 'stepping stones' and perches as they move through the landscape (Hutchinson & Vankat 1997b; Ferguson & Drake 1999; With 2002). For example, a study in Berkshire, England found that larger, evenly dispersed patches of suitable habitat increased the rate of exotic plant spread within the landscape, even when total habitat area was held constant (Bergelson *et al.* 1993).

1.1.4 Description of my study system: New Zealand lowland forests

History and pattern of deforestation in New Zealand

Prior to human settlement, the New Zealand archipelago was almost entirely covered in temperate forest (McGlone 1989; Leathwick 2001). Polynesians arrived in New Zealand approximately 800 years B.P. (Wilmshurst *et al.* 2008) and were responsible for clearing approximately 50% of New Zealand's forest cover (McGlone 1989). Widespread European settlement began in the 1840s, and further deforestation resulted in the loss of over 70% of the original forest cover (Leathwick *et al.* 2003b). Fifty-two percent of the land area has been converted to exotic agricultural production systems, and in many lowland areas indigenous ecosystems are almost completely absent (Norton & Miller 2000). Currently, less than 24% native forest cover remains, and the majority occurs in steep, high rainfall areas, at high altitudes (Leathwick *et al.* 2003b; Ewers *et al.* 2006). Deforestation has been most severe in the drier eastern areas of New Zealand, as these were the most susceptible to fires, however approximately 22% of the forest cover in the relatively wet West Coast region of the South Island has also disappeared (Ewers *et al.* 2006). Where native lowland vegetation is present, the fragments are typically small, isolated, and heavily modified, and are surrounded by agricultural and urban landscapes (Taylor & Smith 1997). Consequently, a large number of lowland species are threatened with extinction, however our knowledge about the processes affecting native species in these remnants is very limited (Miller 2000). Despite the severity of deforestation in New Zealand and potential for significant, ongoing impacts on native biodiversity, few studies have examined the effects of forest fragmentation in New Zealand, and relatively little is known about edge effects on native species (but see Young & Mitchell 1994;

Norton 2002; Montgomery *et al.* 2003; Bach *et al.* 2005; Ohlemüller *et al.* 2006; Ewers *et al.* 2007; Ewers & Didham 2008). In view of this, the Department of Conservation has stated that "understanding the effects of fragmentation of threatened lowland ecosystems" is a high research priority (Anon. 2003).

Characteristics of the New Zealand flora

New Zealand has a relatively small native vascular flora for its size (approximately 2400 species), but a relatively large proportion (>80%) of species are endemic (Wardle 1991; Lee *et al.* 2001). New Zealand occupies the temperate climatic zone, however native forests have many affinities with tropical rainforests, such as complex vertical stratification and a high diversity of lianes and epiphytes (Dawson 1993). The native flora is dominated by long-lived woody perennials, ferns, and bryophytes, and is notable because of the prevalence of distinct, varied juvenile growth forms, lack of deciduousness, and the relatively high level of dioecism (Dawson 1993; Lee *et al.* 2001). Most native plants are adapted to low nutrient conditions, and hence have relatively slow growth rates and slow uptake of nutrients (Craine *et al.* 2006). The native flora is dwarfed by the number of exotic species, with over 25,000 species being introduced (Williams & Cameron 2006). Over 10% of the exotic species are now naturalised (Howell & Sawyer 2006), and the overall rate of naturalisation has increased since European colonisation (Gatehouse 2008). The Department of Conservation currently lists over 320 species of exotic plants as environmental weeds (Howell 2008). Most environmental weeds in New Zealand originate from the Northern Hemisphere (Williams & West 2000). Three quarters of terrestrial weeds were deliberately introduced to New Zealand as ornamental plants, and a further 14% were originally introduced for agriculture, horticulture or forestry (Buddenhagen *et al.* 1998). Only 10% arrived accidentally. Plant families with the highest numbers of invasive species are Poaceae (32 species), Fabaceae (20 species), Asteraceae (17 species) and Rosaceae (14 species) (Williams & West 2000).

Impacts of invasive plants in New Zealand

Invasive plants have major impacts on New Zealand's native species, and understanding these impacts and the mechanisms driving them is essential for conservation and management of native biodiversity (Atkinson & Cameron 1993; Owen 1998; Anon. 2000; Williams & Timmins 2002). The New Zealand Biodiversity Strategy (Anon. 2000) states that "Invasive introduced weeds pose serious threats to ecosystem functioning and the survival of indigenous species in many natural areas, on both public and private land." If uncontrolled, weed invasions could threaten natural

areas covering more than 580,000 ha (Owen 1998). Despite the potential significance of these invasions, relatively little is known about the invasibility of native communities (Wiser & Allen 2006), or the interactions between native and exotic plant species (Anon. 2000). Because of this, the Department of Conservation has stated that "evaluating the processes that make particular native communities vulnerable to invasion" is a high priority for research (Anon. 2003). The naturalised flora of New Zealand is at a very early stage of invasion, with most species having local distributions and small populations, and few species currently occupy anywhere near their full environmental range (Williams & Cameron 2006). The full potential for exotic plant species to invade and spread within natural habitats is still unknown, and the impacts of exotic species on native ecosystems are poorly understood (Atkinson & Cameron 1993; Wiser & Allen 2006).

1.2 THESIS OBJECTIVES

The overall goal of my research was to investigate the effects of habitat fragmentation and invasions on plant communities in native forest fragments, and to examine these processes and potential interactions between them at multiple spatial scales – edge, fragment and landscape. In particular, my research aimed to examine the importance of the amount of native forest cover in the landscape in influencing exotic plant invasions into fragmented forests.

My specific research questions were:

1. How does habitat fragmentation affect plant community composition in native forest fragments?

2. Is there is a relationship between the proportion of forest cover in the landscape and exotic plant invasions into native forest fragments? Is there any evidence for a threshold effect of landscape cover on invasions?

3. Is there a positive relationship between native and exotic plant diversity in fragmented landscapes, or do native and exotic plant species respond differently to forest fragmentation?

4. How do the traits of exotic plant species affect their invasiveness in fragmented landscapes?

5. What mechanisms are driving exotic plant invasions into native forest fragments? Are plant invasions into fragments limited by propagule availability and/or habitat suitability and does landscape cover influence the invasion success of exotic plants in forest fragments?

6. How does forest fragmentation affect native lowland plant communities? Are some species more vulnerable to edge and area effects than others, and what life history traits do they possess?

1.3 THESIS STRUCTURE

This thesis comprises six chapters, four of which have been written in manuscript-style and are intended for publication in peer-reviewed journals. There is some overlap in the methods used for Chapters 2, 3, 4 and 5, so in order to minimise repetition, I have abbreviated some sections of the methods in Chapters 3-5 and referred to the full description of the methods in Chapter 2. The references from each chapter have been combined into one References section at the end of the thesis.

The thesis is organised as a progression of chapters beginning by examining the effects of fragmentation on the species composition of plant communities at multiple spatial scales, then moving on to the role of exotic species traits in influencing their invasiveness in forest fragments, then exploring the mechanisms driving invasions in fragmented landscapes, and finally focusing on the responses of different groups of native plants to edge and area effects.

The chapters are organised as follows:

Chapter 2 investigates the interactions between edge, area and landscape effects on exotic plant invasions in native forest fragments using empirical data collected from fragmented landscapes on the West Coast of the South Island. The role of landscape context in influencing the invasion process is examined, and in particular the importance of the amount of forest cover in the landscape for edge-mediated invasions into forest fragments.

Chapter 3 explores the role of exotic plant traits in influencing their distribution and abundance in forest fragments. The invasion success of exotic plants was determined at both the edge and

interior habitats of forest fragments in order to assess whether different traits contribute to invasiveness in different habitats.

Chapter 4 examines the mechanisms driving exotic plant invasions in fragmented landscapes, and attempts to tease apart some of the inter-correlated factors. The influence of landscape context on edge-mediated invasions was examined at native forest fragments in five landscapes with varying proportions of native forest cover. Experimental addition of exotic plant propagules was used to determine the potential germination and growth rates of exotic plants in native forest fragments, and to assess whether propagule availability and/or habitat suitability may be limiting invasions into fragments.

Chapter 5 discusses the impacts of fragmentation on native plant communities, focusing on area and edge effects in native forest fragments. Edge and area effects were analysed separately for different vegetation tiers, in order to assess whether responses to fragmentation differed spatially within the plant community. The responses of different life forms and dispersal mechanisms to edge and area gradients were also determined, and the importance of life history traits in driving the responses of native plants to fragmentation is discussed.

Chapter 6 summarises the overall conclusions of the thesis and suggests future research directions on the interactions between habitat fragmentation and invasions. I also discuss the implications of my research for the conservation of native species in lowland forest fragments in New Zealand.

Chapter 2 – Interactions between edge, area and landscape effects on exotic plant invasions in fragmented forests

2.1 INTRODUCTION

Habitat fragmentation and biological invasions are major drivers of global biodiversity loss (Vitousek *et al.* 1997; Wilcove *et al.* 1998; Mack *et al.* 2000; Fahrig 2003), and synergistic interactions between these processes have the potential to cause even greater biodiversity loss than either acting alone (Didham *et al.* 2007). Species living in habitat fragments are affected by a range of processes occurring in surrounding landscapes, and are increasingly exposed to the threat of invasive species (Janzen 1983; Davies *et al.* 2001; Hobbs 2001). Disturbance is known to be a key factor promoting invasions, and disturbances caused by fragmentation are likely to make communities more vulnerable to invasion by exotic plants (Sousa 1984; Lewin 1987; Hobbs & Huenneke 1992; Alpert *et al.* 2000; Hobbs 2001). Interactions between fragmentation and invasions can occur at multiple spatial scales, ranging from edge to fragment to landscape (With 2002; With 2004).

Firstly at local scales, the consequences of edge creation (collectively referred to as "edge effects") for plant communities have been well-documented, particularly in forest habitats (Laurance & Yensen 1991; Chen *et al.* 1992; Malcolm 1994; Matlack 1994b; Camargo & Kapos 1995; Murcia 1995; Fox *et al.* 1997; Laurance *et al.* 1998a; Fagan *et al.* 1999; Sizer & Tanner 1999; Ries *et al.* 2004; Harper *et al.* 2005; Marchand & Houle 2006). A number of studies have highlighted the importance of edges as focal sites for exotic plant invasions (Brothers & Spingarn 1992; Fraver 1994; Fox *et al.* 1997; Rose 1997; Meiners & Pickett 1999; Cadenasso & Pickett 2001; Honnay *et al.* 2002; MacQuarrie & Lacroix 2003; Devlaeminck *et al.* 2005; Reemts 2005). Altered conditions at edges may make forest fragments more vulnerable to invasion because they tend to favour the establishment and survival of exotic species (Ranney *et al.* 1981; Brothers & Spingarn 1992; Fox *et al.* 1997; Yates *et al.* 2004). These changes include increased light, temperature and nutrient levels, reduced humidity, increased exposure to wind, grazing, and other disturbances (Saunders *et al.* 1991; Young & Mitchell 1994; Chen *et al.* 1995; Murcia 1995; Fox *et al.* 1997; Duggin & Gentle 1998; Weathers *et al.* 2001; Harper *et al.* 2005). Edges may also have high abundance of invasive species because they tend to intercept airborne particles and seeds, and they are often the first point of contact for organisms dispersing from the matrix (Brothers & Spingarn 1992; Cadenasso & Pickett 2001). Establishment of exotic plants at edges

may lead to their penetration into fragment interiors over time (Fraver 1994), however the physical structure of an edge will influence the invasibility of fragments, as edges with a dense 'curtain' of native shrubs and other vegetation can impede the flow of organisms into fragments (Cadenasso & Pickett 2001; Cadenasso *et al.* 2003).

Secondly at the patch scale, fragment size and shape influence fragment invasibility because they determine the relative amount of edge habitat in a fragment (Janzen 1983; Laurance & Yensen 1991; Ewers & Didham 2006a). Small fragments are likely to be at greater risk of species invasion because proportionally more of the fragment is exposed to edge effects, and they are likely to experience greater levels of disturbance, such as grazing, logging, wind-throw and nutrient enrichment, than larger remnants (Janzen 1983; Hobbs 2001; Stevenson 2004; Echeverría *et al.* 2007; Duncan *et al.* 2008). Long, thin fragments are likely to be more vulnerable to invasion because they have more edge-affected area than circular fragments of the same total area (Collinge 1996; Yates *et al.* 2004). For example, a study in New Zealand found that species richness of exotic weeds in reserves was significantly positively correlated with reserve shape index, indicating that invasion rates were higher in reserves with more complex shapes and thus more edge habitat (Timmins & Williams 1991).

Thirdly at the landscape scale, a number of recent studies have highlighted the importance of landscape context in influencing invasions in fragmented habitats (With 2002; Pauchard & Alaback 2004; With 2004; Deckers *et al.* 2005; Bartuszevige *et al.* 2006; Henderson *et al.* 2006; Duguay *et al.* 2007; Nesslage *et al.* 2007). Landscape context refers to the amount of habitat remaining in a landscape as well as landscape structure, which encompasses the spatial arrangement of fragments and the habitat composition of the landscape matrix (Turner 1989). Landscape context is likely to influence many aspects of the invasion process, including propagule pressure, dispersal of invasive species, and the invasibility of fragments (Hutchinson & Vankat 1997b; With 2002; With 2004; Buckley *et al.* 2006). The amount of habitat remaining in a landscape could influence the abundance of invasive species in fragments because more heavily deforested landscapes are likely to support greater numbers of exotic species, and hence exert higher exotic propagule pressure on fragments (Barlow & Kean 2004; Charbonneau & Fahrig 2004; With 2004). Human activities in the surrounding landscape will also influence exotic propagule pressure, as increased human modification and disturbance are likely to facilitate the establishment and spread of invasive species (Lozon & MacIsaac 1997; Burke & Nol 1998; With 2004; Alston & Richardson 2006; Guirado *et al.* 2007; von Holle & Motzkin 2007). For example, the abundance and diversity of exotic plants tends to increase with human population density and

infrastructure such as roads (Timmins & Williams 1991; Tyser & Worley 1992; Lozon & MacIsaac 1997; Vilà & Pujadas 2001; Pyšek *et al.* 2002; Aragón & Morales 2003; Gelbard & Belnap 2003; Watkins *et al.* 2003; Lundgren *et al.* 2004; Sullivan *et al.* 2004; Bartuszevige *et al.* 2006; Sanz-Elorza *et al.* 2006; Duguay *et al.* 2007; Guirado *et al.* 2007). In addition, landscape structure has been shown to influence the behaviour and movement patterns of some animal pollinators and dispersers, which in turn affect the reproduction and dispersal of invasive plants (van Ruremonde & Kalkhoven 1991; Gosper *et al.* 2005; Buckley *et al.* 2006). Understanding how landscape context affects invasion processes could be crucial for predicting and managing the spread of invasive species in fragmented landscapes (Hutchinson & Vankat 1997b; With 2004), however very few studies have explicitly examined interactions between landscape factors and invasive species (With 2002; Didham *et al.* 2007).

Some authors have noted that the relationship between landscape cover and biotic responses may not be linear, and instead there may be a threshold in habitat cover required for species persistence (known as the "extinction threshold hypothesis") (Lande 1987; Andrén 1994; With & Crist 1995; Fahrig 1998; Lindenmayer & Luck 2005; Frair *et al.* 2008). Below this threshold, connectivity between fragments decreases abruptly, and fragmentation effects become disproportionately more severe (Fahrig 1998, 2002; Lennartsson 2002). Most theoretical studies have predicted that thresholds will occur at 10-30% habitat cover in the landscape, however the threshold will vary according to habitat type, spatial scale of the landscape, and characteristics of the species involved (Andrén 1994, 1997, 1999; Lindenmayer & Luck 2005). Relatively few empirical studies have tested the landscape threshold hypothesis, and conclusions have been mixed, with some studies providing support for the concept (Villard *et al.* 1999; Bascompte & Rodríguez 2001; Radford & Bennett 2004; Radford *et al.* 2005; Dodd *et al.* 2006; Betts *et al.* 2007; Frair *et al.* 2008), while others have found no evidence for threshold effects on ecological patterns (Parker & Mac Nally 2002; Lindenmayer *et al.* 2005). With (2002, 2004) suggested that landscape thresholds could also be important for invasion processes, and predicted that invasion success would be greatest when >20% of the landscape has been disturbed, however to my knowledge, only one study has examined this concept thus far (Nesslage *et al.* 2007). Nesslage *et al.* (2007) quantified the relationship between landscape structure and the spread of the gypsy moth (*Lymantria dispar*) across Michigan, and attempted to identify potential thresholds in landscape structure for invasion success. They examined this relationship using two measures of invasion success and six landscape metrics calculated at three different spatial scales (15, 45, and 75 km^2 landscapes). The study found, however, that thresholds in invasion success did not correspond closely with

thresholds in landscape structure, and suggested that analysis at even larger spatial scales (>75 km^2) may be necessary for highly mobile species such as the gypsy moth.

Fragmentation effects occurring at multiple spatial scales (edge, patch and landscape) may interact with each other, and in turn influence invasion processes in fragmented landscapes. Interactions between area and edge effects have been reported in forest fragments, with the strength of edge effects typically increasing with decreasing fragment size (Malcolm 1994; Didham *et al.* 1998; Barbosa & Marquet 2002; Ewers *et al.* 2007). The most likely explanation appears to be that small fragments have a higher proportion of edge habitat than large fragments, hence they are exposed to the effects of multiple edges (Laurance & Yensen 1991; Malcolm 1994). Interactions between landscape cover and edge effects have also been documented, with several studies indicating that landscape cover can influence the strength of edge effects on predation rates of native species by invasive species (Robinson *et al.* 1995b; Donovan *et al.* 1997; Hartley & Hunter 1998; Lahti 2001; Driscoll & Donovan 2004). For example, in the American Midwest, nest predation rates by introduced cowbirds were higher at edges than in fragment interiors, but only in moderately to highly fragmented landscapes (Donovan *et al.* 1997). To my knowledge, three-way interactions between edge, area, and landscape effects have never been investigated in one study, nor have these effects been examined together in relation to invasion processes. This represents a critical limitation on integrating our understanding of invasion processes over a range of spatial scales, as multi-scale approaches are needed to fully understand the dynamics of systems exposed to plant invasions (Pauchard & Shea 2006).

The overall goal of this study was to investigate the effects of habitat loss and fragmentation on exotic plant invasions, using native forest fragments on the West Coast of the South Island as the study system. The objective was to examine the effects of fragmentation on the composition of plant communities at multiple spatial scales – edge, fragment and landscape – and to investigate potential interactions between these factors. Firstly, I predicted that exotic plant invasions would be greatest at edges (compared to interior habitats), in small fragments (compared to large fragments), and in more heavily deforested landscapes (compared to more intact landscapes). Secondly, I expected that the strength of edge effects on plant communities would vary with fragment size and the amount of forest cover in the landscape, and that these effects would be relatively stronger in small fragments and in heavily deforested landscapes. I also aimed to investigate whether there was any evidence for a threshold in the effects of landscape forest cover on exotic plant invasions, i.e. whether invasions in forest fragments increase markedly below 20-30% forest cover in the landscape.

2.2 METHODS

2.2.1 Study area

The study was carried out in the Grey and Buller Districts on the West Coast of the South Island of New Zealand (42°08' to 42°36' S and 171°25' to 171°46' E, see **Figure 2.1**). The West Coast region as a whole has retained a relatively large proportion of native forest cover (62%) compared to many other regions in New Zealand (Ewers *et al.* 2006), but nevertheless contains landscapes that vary substantially in the amount of forest loss. The Land Environments of New Zealand (LENZ) classification (Leathwick *et al.* 2003b) was used to delineate the boundaries of the study area and identify landscapes with broadly similar physical and environmental and characteristics. The study sites were located within LENZ classes 'M' (Western South Island Recent Soils) and 'O' (Western South Island Foothills and Stewart Island). These classes encompass the alluvial lowlands of the Grey and Waipuna Valleys and Lake Brunner area. The area has a maritime climate with very high rainfall (2500-3000 mm p.a.), mild summers (mean monthly temperature of 15.6°C in January) and cool winters (mean monthly temperature of 7.5°C in July), with approximately 55 days of ground frost per year (NIWA 2007).

The study area occupies a transition zone between the two main forest types which occur in New Zealand: beech forest, dominated by *Nothofagus* spp. (Fagaceae) and podocarp-broadleaved forest, dominated by conifers in the Podocarpaceae. Study sites contain a mixture of several co-dominant species, including *Nothofagus fusca* (red beech), *N. menziesii* (silver beech) and *N. truncata* (hard beech), and the podocarps *Dacrycarpus dacrydioides* (kahikatea), *Dacrydium cupressinum* (rimu) and *Prumnopitys ferruginea* (miro). Prior to human settlement of New Zealand, the West Coast region would have been almost entirely covered in native forest (Leathwick 2001). Elevated and steep land is still largely covered in native forest, however lowland areas (i.e. below 300 m a.s.l) have been extensively deforested to make way for agriculture. The dominant land use in these areas is pastoral farming, with sheep and beef being the main farm types, followed by dairy and deer. Exotic plantation forests occupy only 2% of the West Coast region (Ewers *et al.* 2006).

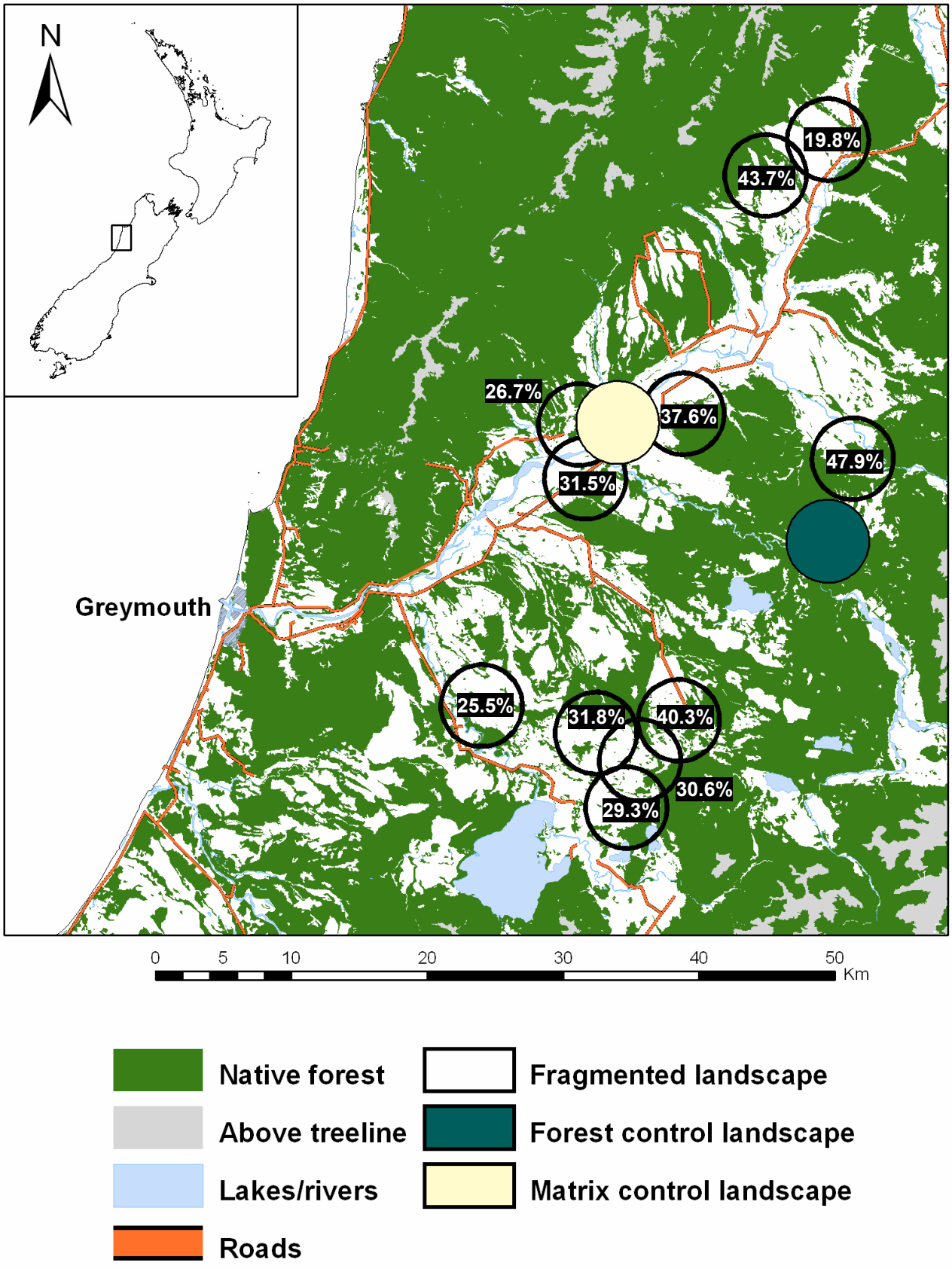


Figure 2.1. Map of the study area in the Grey and Buller Districts, West Coast, New Zealand (42°08' to 42°36' S and 171°25' to 171°46' E). Edge gradients were sampled at native forest fragments in 11 fragmented landscapes and 2 control landscapes (circles with a 3 km radius). Native forest cover ranged from 19.8% to 47.9% in the fragmented landscapes. Land cover was determined from the NZ Land Cover Database version 2 (MfE 2004).

2.2.2 Landscape and fragment selection

The goal of the study was to investigate the effects of forest fragmentation on exotic plant invasions at multiple spatial scales: edge, fragment and landscape. The approach was to select landscapes that varied in the proportion of native forest cover and contained forest fragments in standardised size categories, as this would also allow me to examine the effects of forest cover on edge-mediated invasions by exotic plants, as well as the effects of fragment area in each landscape. Native forest within the study area was examined in a geographic information system (GIS) using data from the Land Cover Database Version 2 (LCDB2) (MfE 2004), analysed with ArcGIS 9.1 (ESRI 2005). The LCDB2 is a thematic classification of New Zealand's land cover developed from LANDSAT 7 ETM+ satellite images acquired between September 2001 and March 2002. Native forest comprised two LCDB2 classes: 'Indigenous forest' (mature indigenous forest) and 'Broadleaved indigenous hardwoods' (successional forest containing a mix of broadleaved seral hardwood species).

Potential landscapes were defined by overlaying a 1 x 1 km grid of 1258 points on the study area and creating a circular landscape with a radius of 3 km (an area of 2827.43 ha) around each point. A 3 km radius was mainly chosen because of the geography of the study area, where lowland landscapes occupy relatively narrow river valleys constrained by mountain ranges. This scale was also within the range used by other studies investigating the effects of landscape context on species diversity (e.g. Austen *et al.* 2001; Steffan-Dewenter 2003; Charbonneau & Fahrig 2004; Gabriel *et al.* 2005; Gorresen *et al.* 2005; Lindborg 2007), and is likely to encompass the maximum dispersal distances of most plant species (Kumar *et al.* 2006). It is acknowledged, however, that *a priori* selection of landscape size (in order to detect a landscape treatment effect) for community-level studies is problematic, as responses to spatial scale will inevitably vary among species (Turner 1989; Kumar *et al.* 2006).

The percentage of native forest cover in each of the 1258 landscapes was calculated, and ranged from 2.3% to 93.4%, with 2 to 52 forest fragments per landscape. The aim was to select landscapes which varied in the proportion of native forest cover and also contained at least one fragment in each of the four standardised size categories: 0.5-2.0 ha, 2.0-8.0 ha, 8.0-32.0 ha and >32.0 ha (based on a $\log_2$ scale). The majority of fragments in the study area were <32 ha in size, therefore a logarithmic scale ensured that fragments from a range of sizes were sampled in each landscape. Stratified sampling was used to select 11 landscapes which ranged in native forest cover from 19.8% to 47.9% and contained four fragments in the desired size categories (44

fragments in total) (see **Table 2.1**). Potential fragments identified from the GIS were then visited in the field to assess their suitability. Fragments had to meet certain criteria for selection: they had to be below 200 m a.s.l (i.e. lowland forest), on level ground (slopes less than 5°), adjacent to pasture, and have a reasonable cover of ground vegetation (not more than 50% bare ground). Due to the limited number of suitable fragments in each landscape, several fragments outside these size categories had to be used (**Table 2.1**). During the field visits, I discovered that the some of the selected forest fragments had been drawn incorrectly in LCDB2, so the boundaries of these polygons were redrawn using ArcGIS 9.1 (ESRI 2005), and these corrected polygons were used in subsequent analyses.

Two 'control' landscapes at both ends of the habitat loss continuum were also selected, with four 'pseudo fragments' delineated at haphazardly-located points in each. The purpose of the controls was to provide reference plant communities which indicated the degree of exotic invasion in both intact and entirely deforested landscapes in the study area. The 'Matrix Control' landscape contained 9.2% native forest cover and was located in matrix habitat (pasture) in the Grey Valley (**Figure 2.1**). The 'Forest Control' landscape, containing nearly intact forest cover (85.8%), was located on Department of Conservation land in the upper Ahaura Valley, as this was the largest area of continuous forest below 300 m a.s.l. in the study area.

2.2.3 Selection of edge gradients

In order to minimize variability in boundary types, the 44 fragments were selected to have similar matrix vegetation (i.e. forest edges adjacent to pasture or other non-woody vegetation only). Plant communities were sampled on north-facing edges only (ranging from NW to NE) as these typically display the strongest edge gradients in microclimate and species composition in southern hemisphere regions (Fraver 1994; Young & Mitchell 1994; Chen *et al.* 1995). The edge of each forest fragment was defined by the limit of the continuous tree canopy (Harper *et al.* 2005).

Rectangular survey plots measuring 15 x 2 m were aligned with the long axis parallel to the forest edge on a logarithmic (base 2) scale up to 128 m inside each fragment (coded as -0.33, -2, -4, -8, -16, -32, -64, -128 m) and up to 8 m into the adjacent matrix habitat (+0.33, +2, +4, +8 m), as well as up to 8 distances at each of the Matrix and Forest Control sites, giving 516 vegetation sampling plots in total. The edge gradient was sampled on both sides of the forest edge, as edge effects are often asymmetrical across habitat boundaries (Ewers & Didham 2006b; Fonseca & Joner 2007). A logarithmic scale was chosen for sampling because changes in microclimate, vegetation structure,

species diversity and abundance occur most rapidly immediately adjacent to the edge (Young & Mitchell 1994; Fox *et al.* 1997; Sizer & Tanner 1999; Davies-Colley *et al.* 2000). The length of edge gradient able to be sampled varied among fragments, and larger edge distances were sequentially dropped according to the size and shape of each fragment (with a minimum of five forest interior plots at each fragment) (see **Table 2.1**). One edge gradient per fragment was sampled to avoid pseudoreplication. Areas with >50% non-vegetated cover (e.g. streams, bare ground, bogs) were avoided, with plots being moved parallel to the edge by up to 10% of their respective distance from the edge in these situations. Major canopy gaps and tree falls were also avoided. Control sites were surveyed along pseudo edge gradients so that the real edge gradients in fragmented landscapes could be compared to the expected amount of variation in species turnover without edge influence. Forest Control sites were located in interior forest habitat and plots were a minimum of 1700 m away from an edge adjacent to open pasture matrix. The lengths of edge gradients sampled at the four Forest Control sites were 32, 64, 128, and 128 m respectively. Matrix Control sites were located in open pasture habitat and plots were at least 130 m from the nearest native forest fragment. The lengths of edge gradients sampled at the four Matrix Control sites were 32, 64, 64, and 128 m respectively.

2.2.4 Vegetation surveys

Vegetation at the study sites was surveyed from December 2004 to May 2005, November 2005 to May 2006 and January 2007. The percent cover of native and exotic vascular plant species in each plot was estimated in two height tiers: ground (0.0-0.5 m) and shrub (0.5 – 2.0 m). These lower height tiers represent the focal plant community for this study because the majority of exotic species occur only below 2 m in height, and forest canopies are dominated by native species. Species not able to be identified in the field were collected, and specimens were later identified using taxonomic keys (Allan 1961; Healy & Edgar 1980; Webb *et al.* 1988; Edgar *et al.* 2000) or by the Landcare Research Plant Identification Service (Lincoln, Canterbury, New Zealand). Because the depth varied among the different height tiers, percent cover data were converted to overall cover scores using the formula (David Norton, pers. comm.):

$$\text{Cover score} = \sum \%\text{cover} \times \log_{10}(\text{tier depth})$$

The degree of exotic invasion was measured by percent exotic richness and percent exotic cover. Percent exotic cover provides an indication of the degree to which plant biomass is dominated by exotics, as the impact of invaders on the native plant community is likely to be proportional to their biomass relative to native species (Lundholm & Larson 2004).

Table 2.1. The percentage of native forest cover in each of the 11 fragmented landscapes (3 km radius), fragment area, and length of edge gradient sampled at each fragment. Each landscape contained fragments in four size classes (0.5-2.0, 2.0-8.0, 8.0-32.0, and >32.0 ha). Plots at the edge were coded as -0.33 and +0.33 in the forest and matrix respectively for data analysis.

Landscape forest cover	Site name	Fragment Size class	Area (ha)	Distance from the forest edge (m) Forest -128	-64	-32	-16	-8	-4	-2	-0.3	Matrix 0.3	2	4	8
19.8%	Maimai2	0.5-2 ha	2.1												
	King6	2-8 ha	5.7												
	Mawhera	8-32 ha	13.7												
	Maimai	>32 ha	46.5												
25.5%	Blair2	0.5-2 ha	1.9												
	Blair6	2-8 ha	6.0												
	Blair20	8-32 ha	20.6												
	Blair32	>32 ha	330.0												
26.7%	LittleB	0.5-2 ha	1.6												
	BerryP	2-8 ha	2.4												
	BerryA	8-32 ha	12.2												
	Little	>32 ha	53.7												
29.3%	Weka2	0.5-2 ha	1.7												
	Weka6	2-8 ha	6.5												
	Weka17	8-32 ha	17.1												
	Weka97	>32 ha	96.6												
30.6%	Ruru2	0.5-2 ha	1.6												
	Ruru4	2-8 ha	4.0												
	Ruru10	8-32 ha	10.2												
	Ruru126	>32 ha	124.7												
31.5%	HahnC	0.5-2 ha	0.8												
	Savage	2-8 ha	5.9												
	HahnB	8-32 ha	9.2												
	Hahn32	>32 ha	17.9												
31.8%	BellHill2	0.5-2 ha	1.0												
	BellHill5	2-8 ha	5.8												
	BellHill10	8-32 ha	10.4												
	BellHill112	>32 ha	103.8												
37.6%	McInroeC	0.5-2 ha	1.4												
	McInroe	2-8 ha	8.8												
	McInroeB	8-32 ha	13.0												
	DOC62	>32 ha	39.3												
40.3%	Souters2	0.5-2 ha	0.3												
	Souters4	2-8 ha	3.8												
	Souters23	8-32 ha	25.7												
	Souters79	>32 ha	78.7												
43.7%	Thompson09	0.5-2 ha	0.9												
	Thompson6	2-8 ha	6.2												
	Somerville11	8-32 ha	11.4												
	Somerville77	>32 ha	77.5												
47.9%	FergusonC	0.5-2 ha	1.3												
	Ferguson71	2-8 ha	4.6												
	FergusonB	8-32 ha	11.8												
	DOC72	>32 ha	56.5												
Total number of plots at each edge distance				**10**	**25**	**41**	**44**	**44**	**44**	**44**	**44**	**44**	**43**	**40**	**36**

2.2.5 Environmental variables

In total, 152 environmental variables were measured as potential correlates of plant responses to forest fragmentation (**Table 2.2**). These consisted of 9 habitat fragmentation treatment variables, 132 variables describing environmental variation among plots, fragments and landscapes, and 11 variables representing the potentially confounding effects of aspect, altitude and spatial autocorrelation on plant species composition.

Table 2.2. Descriptions of the 152 environmental variables calculated for each of the 516 sampling plots. Data sources: LCDB2 = Land Cover database version 2 (MfE 2004). LENZ = Land Environments of New Zealand (Leathwick *et al.* 2003b). Topomap = New Zealand Map Series 260, 1:50,000, Land Information New Zealand, Wellington. Soil Bureau = New Zealand Soil Bureau Map (Mew & Ross 1980). DEM = New Zealand 25 m digital elevation model.

Code	Description	Units	Data source
Treatment variables			
Landscap	native forest cover within 3 km radius landscape	%	LCDB2
LogArea	Log_{10} (fragment area + 1)	ha	LCDB2
Edgedist	Log_2 distance from edge (coded as negative inside forest)	m	
LscpArea	Landscape-area interaction (Landscap x LogArea)		
LscpEdge	Landscape-edge distance interaction (Landscap x Edgedist)		
AreaEdge	Area-edge distance interaction (LogArea x Edgedist)		
LxAxE	Landscape x LogArea x Edgedist interaction		
FORdummy	Deep forest dummy (Forest control sites = 1)	binary	
MATdummy	Deep matrix dummy (Matrix control sites = 1)	binary	
Site and plot attributes			
ShapeInd	Fragment shape index		LCDB2
Beef	Adjacent farm type = beef	binary	Field survey
Dairy	Adjacent farm type = dairy	binary	Field survey
Deer	Adjacent farm type = deer	binary	Field survey
SheepBef	Adjacent farm type = sheep and beef	binary	Field survey
Canopy	% canopy cover	%	Field survey
Baregrnd	% cover bare ground	%	Field survey
Moss	% cover moss	%	Field survey
RaisedM	% cover raised microsites	%	Field survey
Grazing	Grazing intensity (0=none, 1=low, 2=med, 3=high, 4=v.high)	0-4 scale	Field survey
LiveTree	Basal area of native trees	m^2/ha	Field survey
WeedTree	Basal area of exotic trees	m^2/ha	Field survey
DeadTree	Basal area of dead trees	m^2/ha	Field survey
TreeDiv	Tree species richness (woody spp >3 cm dbh)		Field survey
DACcup	Upper tiers cover score for *Dacrydium cupressinum*		Field survey
DACdac	Upper tiers cover score for *Dacrycarpus dacrydioides*		Field survey
NOTfus	Upper tiers cover score for *Nothofagus fusca*		Field survey
NOTmen	Upper tiers cover score for *Nothofagus menziesii*		Field survey
NOTtru	Upper tiers cover score for *Nothofagus truncata*		Field survey
QUIacu	Upper tiers cover score for *Quintinia acutifolia*		Field survey
WEIrac	Upper tiers cover score for *Weinmannia racemosa*		Field survey
SaplingN	Number of saplings (>1.35 m tall, <3 cm dbh)		Field survey
SaplingD	Sapling species richness		Field survey
SoilpH	Soil pH	0-14	Soil samples
SoilP	Soil olsen soluble phosphorus	P ug/mL	Soil samples
SoilOM	Soil organic matter	% w/w	Soil samples

Code	Description	Units	Data source
SoilN	Soil total nitrogen	% w/w	Soil samples
SoilCN	Soil carbon/nitrogen ratio	(ratio)	Soil samples
Drainage	Drainage class (2 = poor, 4 = imperfect, 6 = good)	2-6 scale	Soil Bureau
Tmin	Mean minimum temperature of coldest month	°C	LENZ
Junes	Mean winter solar radiation	$MJ.m^{-2}$/day	LENZ
Vpd	October vapour pressure deficit	kPa	LENZ
R2pet	Monthly water balance ratio	(ratio)	LENZ
LENZ75	LENZ level 4 class = M1.1a	binary	LENZ
LENZ94	LENZ level 4 class = M2.1a	binary	LENZ
LENZ96	LENZ level 4 class = O3.1d	binary	LENZ
LENZ123	LENZ level 4 class = O1.4a	binary	LENZ
LENZ150	LENZ level 4 class = O3.1c	binary	LENZ
Landscape variables			
NND	Distance to nearest native forest (nearest neighbour distance)	m	LCDB2
NearBuil	Distance to nearest building	m	Topomap
NearRiv	Distance to nearest river	m	Topomap
NearRoad	Distance to nearest road/railway	m	Topomap
– calculated within 6 landscape sizes with radii of 256, 512, 1024, 2048, 4096, 8192 m			
FNum	No. of native forest fragments	no./km^2	LCDB2
Buil	No. of buildings per km^2	no./km^2	Topomap
Riv	Length of rivers per km^2	m/km^2	Topomap
Road	Length of roads and railways per km^2	m/km^2	Topomap
Conn	Forest connectivity index		LCDB2
Edge	Edge density	km/km^2	LCDB2
LDiv	Landscape diversity index		LCDB2
AX1	Axis 1 scores of a DCA of land cover		LCDB2
AX2	Axis 2 scores of a DCA of land cover		LCDB2
AX3	Axis 3 scores of a DCA of land cover		LCDB2
AX4	Axis 4 scores of a DCA of land cover		LCDB2
NatF	Native forest cover	%	LCDB2
NatS	Native shrubland cover	%	LCDB2
ExoG	Exotic grassland cover	%	LCDB2
ExoW	Exotic woody vegetation cover	%	LCDB2
Confounding variables			
Altitude	Altitude	m.a.s.l.	DEM
Aspect	Aspect	°	Field survey
Lat	Latitude = N from NZ grid ref/1000	1000 m	Field survey
Long	Longitude = E from NZ grid ref/1000	1000 m	Field survey
LatLong	Lat x Long (spatial autocorrelation variable)		
Lat2	Lat^2 (spatial autocorrelation variable)		
Long2	$Long^2$ (spatial autocorrelation variable)		
Lat3	Lat^3 (spatial autocorrelation variable)		
Long3	$Long^3$ (spatial autocorrelation variable)		
Lat2Long	Lat^2Long (spatial autocorrelation variable)		
Long2Lat	$Long^2Lat$ (spatial autocorrelation variable)		

Treatment variables

The treatment variables comprised fragmentation variables representing spatial structuring of native forest habitat at three scales: edge, fragment and landscape. Distance from the forest edge was $\log_2$ transformed and coded as negative or positive depending on whether the plot was in the forest or matrix respectively (Ewers & Didham 2006b). Fragment area was $\log_{10}$ transformed. Landscape was defined by the percentage of native forest cover in each of the 13 treatment landscapes (circles with a 3 km radius), and ranged from 9.2% to 85.8% (see **Table 2.1**). Binary 'dummy' variables (coded with either zero or one) were created for each of the Control sites (FORdummy and MATdummy). Interactions between edge and area effects are known to occur (Ewers *et al.* 2007), therefore two- and three-way interactions between the treatment variables were included (calculated by multiplying their respective values together).

Fragment and plot attributes

A shape index was calculated for each forest fragment using the equation from Patton (1975):

$$\text{Shape index} = P/(200(\pi * A)^{0.5})$$

where P is the perimeter (m) and A is the area (ha) of the forest fragment. Perfectly circular fragments have a shape index of 1, whereas more complex shapes will have correspondingly higher values. Matrix control sites were arbitrarily assigned a shape index of 1.

Fragments were surrounded by a range of different pastoral farm types, therefore the type of grazing adjacent to the sampled edge was categorized into four binary variables: beef, sheep and beef, dairy, or deer.

Percentage canopy cover calculated from hemispherical photographs was used as a surrogate for light intensity, as this method is significantly faster than direct measurements of photosynthetically active radiation (PAR) or photosynthetic photon flux density (PPFD) using light sensors, and is known to be highly correlated with them (Comeau *et al.* 1998; Engelbrecht & Herz 2001). Comparison with direct solar radiation measurements by light sensors along edge gradients in five fragments confirmed that canopy cover is a valid surrogate for light intensity in this study (Pearson correlation, $n = 32$, $r = -0.845$, $p < 0.001$) (see Ewers *et al.* 2007 for a description of the light sensors). Hemispherical photographs were taken in each plot using a Nikon Coolpix 5700 digital camera with a FC-E9 fisheye lens (183° angle of view). The camera was mounted approximately 1 m off the ground with a tripod and aligned to magnetic north.

Photographs were taken during cloudy conditions to minimize the effect of sun flecks and variability in the amount of sunlight between plots. The aperture was set at F/7.1 and shutter speed to 1/15 second in order to standardise the exposure. Canopy cover percentages were calculated from the hemispherical photographs using Gap Light Analyser version 2 software (Frazer *et al.* 1999).

The percent cover of moss and bare ground in each plot was estimated in order to characterize the ground conditions. The percent cover of 'raised microsites' such as tree bases and fallen logs was recorded, as these are important germination sites for both native and exotic plants because they receive more light and experience less competition with ground cover vegetation than the forest floor (Rogers 1989). Grazing by livestock is thought to facilitate exotic plant invasions in forest remnants (Hobbs 2001; Smale *et al.* 2005; Dorrough *et al.* 2006; Vavra *et al.* 2007), therefore grazing intensity per plot was estimated on a scale ranging from zero (no evidence of grazing by livestock) to four (high density of livestock present). The level was estimated from the number of stock observed, visible damage to vegetation, hoof prints or pugging, and the density of faeces.

The structure of vegetation at forest edges can affect edge-mediated invasions by plants (Cadenasso & Pickett 2001; Bartuszevige *et al.* 2006), so a number of variables reflecting vegetation density were included as predictors: the basal area of live native and exotic trees (dbh >4 cm), the total basal area of standing dead trees, and the number of saplings (woody species >1.35 m in height) and tree ferns (Cyatheaceae and Dicksoneaceae). Species richness of trees and saplings were also included. Plant species composition in the lower tiers may be related to composition in the upper tiers, therefore cover scores (see **section 2.2.4** for explanation) of the dominant species in the sub-canopy (2 – 10 m) and canopy (>10 m) tiers were included as environmental variables. The dominant canopy species comprised two podocarp species, *Dacrydium cupressinum* and *Dacrycarpus dacrydioides,* three species of beech, *Nothofagus fusca, N. menziesii,* and *N. truncata,* and two common tree species on the West Coast, *Quintinia acutifolia,* and *Weinmannia racemosa*.

Soil characteristics and nutrient availability are major drivers of plant species composition and invasions by exotic plants (Allcock 2002; King & Buckney 2002), therefore a number of soil variables were measured in each plot. Soil samples were taken in each fragment at 16 m from the forest edge using a soil auger driven to a depth of 20 cm. Additional samples were taken at five other edge distances in one fragment (in the 2-8 ha size category) in each landscape (+2, -1, -4, -8, and -32 m from the edge). A minimum of six cores were taken at each position and bulked.

Samples were air dried, then ground through a 2 mm sieve. Total carbon, phosphorus, nitrogen, organic matter content and pH were determined by Analytical Research Laboratories Ltd, Napier, New Zealand. Soil phosphorus was measured using Olsen's method (Olsen *et al.* 1954). Total nitrogen was analysed with a LECO analyser using the Dumas method (Petit *et al.* 2004), where soils are introduced into a combustion furnace and oxidised in a pure stream of oxygen. The subsequent gas stream is analysed for nitrogen dioxide by a thermal conductivity detection cell and the results expressed as total nitrogen. Total carbon was analysed by the combustion method using a LECO Analyser. Organic matter content was calculated from organic carbon using a standard mathematical conversion (Peverill *et al.* 1999).

New Zealand Soil Bureau maps (Mew & Ross 1980) were used to estimate the soil drainage level in each plot, which ranged from poor (2 – Kumara, Maimai soils), imperfect-poor (3), imperfect (4 – Ahaura mottled phase, Carton Hill, Moana soils), good-imperfect (5), to good (6 – Ahaura, Hochstetter, Hokitika, Ikamatua soil types). Forest Control sites had very poor drainage (Rotokohu soils), but this drainage category was not included as a predictor because it was identical to the Forest Control dummy variable (FORdummy).

Study sites occupied five LENZ level 4 classes (Leathwick *et al.* 2003b): M1.1a, M2.1a, O3.1c, O3.1d and O1.4a, and these were included as five binary variables (see **Appendix 1** for a description of the classes). Four macroclimatic variables from the underlying layers of LENZ – mean minimum temperature of the coldest month, mean winter solar radiation, October vapour pressure deficit and monthly water balance ratio – were also included because of their importance for the distribution of New Zealand tree species (Leathwick *et al.* 1998).

Landscape-level variables

In addition to the landscape treatment (3 km radius), a range of landscape-level variables were calculated for each plot using GIS analysis of the NZ Land Cover database (MfE 2004) and digitized layers of New Zealand topographic maps (New Zealand Map Series 260, 1:50,000. Land Information New Zealand, Wellington) (see **Table 2.2**). The degree of isolation of each fragment was measured by the nearest neighbour distance (NND), which was calculated as the distance from each plot to the edge of the nearest other native forest fragment using the Distance Matrix extension in ArcView GIS 3.2a (ESRI 1996). Distances to the nearest building and road or railway were calculated using the same tool. These variables were included because they are likely to be correlated with the degree of human modification and disturbance in the landscape.

The remaining landscape variables were calculated at six different spatial scales using concentric circles with radii of 256, 512, 1024, 2048, 4096 and 8192 m (based on a $\log_2$ scale, as this scale was also used for edge distances and fragment size classes). Landscapes were centred on each of the 516 field survey plots.

Forest edge density was calculated by dividing the total length of edge of native forest fragments in each landscape (in km) by the area of the landscape (in km^2). A forest connectivity index (C) was calculated for each landscape using the equation from Steffan-Dewenter (2003):

$$C = \sum e^{-dij} A_j$$

where A_j is the area of neighbouring forest fragments in the surrounding landscape and d_{ij} is the distance (in km) from the central forest fragment *i*. Increasing C corresponds to less isolated or better connected study sites. The forest connectivity index was log transformed ($\log_{10}C + 1$).

The study area encompassed 30 different LCDB2 classes, and individual landscapes contained between one (256 m radius) and 26 (8192 m radius) classes. A diversity index (H') was calculated for each landscape using the Shannon-Weiner index (Krebs 1999):

$$H' = - \sum p_i \ln p_i$$

where p_i is the proportion of the landscape covered by the i^{th} land cover type.

Detrended correspondence analysis (DCA), a multivariate ordination technique, was used to characterise the major patterns in land cover classes in each landscape (Hill & Gauch 1980). The total area of each land cover class in each landscape (derived from the LCDB2) was entered as the species data in the DCA. 'Rare' land cover classes were downweighted and detrending by segments was used. The first four DCA axes each explained a significant amount of variation in the land cover data, so these were all included as environmental variables. The percentages of native forest, native shrubland, exotic woody vegetation, and exotic grassland in each landscape were calculated. Native shrubland comprised two LCDB2 classes: 'grey shrubland' and 'manuka and kanuka'. Exotic woody vegetation comprised six land cover classes: 'deciduous forest', 'exotic forest', 'gorse and broom', 'pine forest – closed canopy', 'pine forest – open canopy' and 'major shelterbelts'. Exotic grassland was made up of both high- and low-producing exotic grassland. Nearest neighbour distance, i.e. the distance from each plot to the edge of the nearest native forest fragment, was calculated using the Distance Matrix extension in ArcView GIS 3.2a (ESRI 1996). The distances to the nearest building, river, and road or railway were calculated using the same tool. These features were included because they are associated with disturbances

and are important foci for exotic plant invasions (Timmins & Williams 1991; Vilà & Pujadas 2001; Lundgren *et al.* 2004). Roads and rivers may act as corridors and facilitate the spread of exotic plants in the landscape (Tyser & Worley 1992; Parendes & Jones 2000).

Confounding variables

The site selection procedure aimed to minimize variation between the fragments and edges sampled, however there was some potential variability among sites for several key variables. Altitude (determined from the New Zealand 25 m digital elevation model) and aspect were considered to be potentially confounding variables. The effect of spatial autocorrelation on community composition was assessed using linear, quadratic and cubic combinations of latitude and longitude co-ordinates from the New Zealand Map grid (NZMG). NZMG values were recoded and then truncated to the nearest 1000 m in order to avoid removing the fine-scale spatial autocorrelation within edge gradients, as described by Ewers *et al.* (2007).

2.2.6 Statistical analyses

Ordinations of plant community composition

Canonical correspondence analysis (CCA), a direct gradient (or constrained) analysis technique, was used to explore the relationship between plant species composition and the measured environmental variables (ter Braak 1986, 1987). CCA extracts the dominant gradients in species composition with the constraint that they must be linear combinations of the independent variables. CCA was used instead of linear ordination methods such as RDA because gradient lengths were relatively long (Hill & Gauch 1980; Lepš & Šmilauer 2003).

Prior to the CCA, the degree of inter-correlation between the environmental variables was determined with Pearson correlations (Statistica 7.1, StatSoft 2006). Some of the variables were highly inter-correlated ($r > 0.85$, e.g. Conn4096 and Conn8192), therefore one of the pair of variables was discarded prior to the ordination analysis. Following this, 146 environmental variables were entered into a preliminary CCA and forward selection was used initially to determine whether any of the 11 potential confounding variables (Aspect, Altitude and the nine spatial autocorrelation variables) explained a significant amount of the variance in the plant species data. If so, then these significant variables were partialled out of subsequent ordination analyses as covariables. A partial CCA was then carried out and forward selection was repeated

with 135 environmental variables (non-significant confounding variables were omitted). In the forward selection procedure, a Monte Carlo test (with 9999 random permutations) was used to test whether each variable explained a significant amount of the variation in plant species composition, in addition to the variables already selected. A Bonferroni-corrected significance level of $p = 0.0003$ was used in the forward selection (i.e. $p = 0.05/146$ environmental variables), in order to minimise the chance of Type I error resulting from the large number of environmental variables being tested.

Because an arch effect was observed in the preliminary correspondence analysis, detrended canonical correspondence analysis was used to carry out the final constrained ordination (pDCCA) (Lepš & Šmilauer 2003). Downweighting of rare species, detrending by second order polynomials, and bi-plot scaling were selected. A Monte Carlo test with 999 random permutations was used to test the significance of the first canonical axis and the final set of predictor variables in the pDCCA (i.e. whether the ordination axes adequately explain the variation in the species data). The marginal and conditional eigenvalues for each environmental variable were used to assess the strength of the effect of each variable on plant species composition: the marginal effect is the independent effect of a variable on the response variable (i.e. added first in the model), whereas the conditional effect is the additional effect of a variable after accounting for the effects of the other environmental variables. Intra-set correlations were used to assess the relationship of the environmental variables with each pDCCA axis, as these tend to be a more stable measure than the inter-set correlations (ter Braak 1987). Intra-set correlations between the environmental variables and ordination axes were calculated by multiplying the inter-set correlations by the total species-environment correlation for each axis (Lepš & Šmilauer 2003). CANOCO 4.02 software was used to carry out all the ordinations (ter Braak 1997-1999).

The first canonical axis from the pDCCA represented the main gradient in plant community composition in the study area, therefore pDCCA axis 1 scores were used to analyse plant community responses to the environmental variables. The degree of exotic invasion in the plant community was examined using Pearson correlations between pDCCA axis 1 scores and percent exotic richness and percent exotic cover in Statistica 7.1 (StatSoft 2006).

Edge response at each fragment

The strength of edge effects on plant community composition (axis 1 scores from the pDCCA) was determined with edge response functions calculated using the method described in Ewers &

Didham (2006b). Edge responses at control sites were also calculated in order to indicate the amount of underlying variation in responses not attributable to edge gradients. A program run in R 2.4.1 (R Core Development Team 2006) was used to fit continuous functions for response variables along edge gradients from matrix habitat into fragment interiors (Ewers & Didham 2006b). The program determines the best fit model out of five models of increasing complexity, i.e. the model with the lowest Akaike's information criterion (AIC) value. Models are fitted in the following order: null, linear, exponential, logistic, and unimodal. The best model defaults to the null model and is only replaced if a model with a better fit also explains significant variance ($p<0.05$).

As Ewers & Didham (2006b) explain, the logistic and unimodal models allow a number of important edge response parameters to be calculated at each fragment, for example the slope and magnitude of the response. The logistic model is fitted when the response (y) follows a sigmoidal shape with asymptotes at the extreme ends of the gradient. The equation for the logistic model is:

$$y = \beta 0 + \frac{\beta 1 - \beta 0}{1 + e^{(\beta 2 - D)\beta 3}}$$

where D = distance to the forest edge, β0 = asymptote in the fragment interior, and β1 = asymptote in the matrix, β2 = mid penetration point, β3 = slope.

Interactions between edge, area and landscape effects on plant community composition

Two parameters from the fitted logistic edge response functions were used to examine the interactions between treatment effects on plant species composition: β3 (slope) and β0 (the first asymptote). The first asymptote of the logistic function (β0) described above gives the expected value of the response variable when it has reached equilibrium in the fragment interior (i.e. fragment interior plant community composition). High β3 values indicate that plant species composition changes steeply along the edge gradient, whereas low β3 values indicate a shallow change in species composition along the edge gradient. In order to visualise the complex interactions between edge, area and landscape effects on plant species composition, the β0 and β3 values for each fragment (i.e. edge effects at each fragment) were graphed against the percentage of native forest cover in the landscape, with fragments categorised into four size classes (to display the area effect). Linear regression lines are shown for each fragment size class in order to illustrate the nature of the interaction between area and landscape cover, however fragment area (a

continuous variable) was used to determine the significance of the area effect in the pDCCA and fragment size class was not used in the analysis.

The logistic model could not be fitted to edge responses at three fragments because the asymptote in the matrix could not be found (the linear model was chosen as the best model for these fragments). This indicates that species composition had not reached equilibrium in the matrix, and suggests that the distance sampled into the matrix may have been too short at these fragments.

Edge, area and landscape effects on percent exotic species richness and percent exotic cover

The effects of the treatment variables on percent exotic species richness and percent exotic cover were analysed using generalised linear models (GLMs) in R 2.4.1 (R Development Core Team 2006). The treatment variables were entered sequentially in the GLMs, with landscape (percent native forest cover in the landscape) entered first, followed by fragment area, then distance from the forest edge, then the two-way (LscpArea, LscpEdge and AreaEdge) and three-way interaction terms (LxAxE). Type I sums of squares was used to assess the significance of the treatment effects on the response variables – i.e. the area effect was determined after accounting for the effect of landscape forest cover, and the edge effect was determined after accounting for the effects of area and landscape. Two potential confounding variables (Altitude and Aspect) were entered ahead of the treatment variables in the GLMs, in order to partial out their effects on the response variables.

2.3 RESULTS

2.3.1 Plant community responses to edge, area and landscape treatments

The plant community in this study comprised 221 native (see **Appendix 2**) and 108 exotic plant species (see **Appendix 3**). The preliminary CCA revealed that three of the potential confounding variables (Altitude, Long and Long2Lat) explained a significant amount of the variance in plant species composition among plots, therefore these were partialled out of subsequent ordination analyses as covariables. After the forward selection procedure in pCCA, 70 environmental variables (including all 9 treatment variables) were found to explain a significant amount of the variation in plant species composition, and these comprised the predictors in the final pDCCA. The pDCCA results revealed that plant species composition was strongly related to the measured environmental variables, as the first pDCCA axis and final set of predictor variables explained significant variation in the plant species data (**Table 2.3**). The first four canonical axes explained 7.5%, 3.3%, 2.7% and 2.5% of the species variation respectively.

Table 2.3. Results from a partial detrended canonical correspondence analysis (pDCCA) of plant community composition (<2 m in height) in 516 plots. 70 environmental variables were entered in the pDCCA and the effects of three significant covariables (Altitude, Long, Long2Lat) were partialled out. The sum of all unconstrained eigenvalues is after fitting the covariables. Percentages are taken with respect to residual variances i.e. variances after fitting the covariables. A Monte Carlo procedure with 999 random permutations was used to test the significance of the first canonical axis and all canonical axes in the pDCCA.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.767	0.338	0.277	0.255	10.593
Lengths of gradient	0.978	0.876	0.851	0.823	
Species-environment correlations					
Cumulative percentage variance					
of species data	7.5	10.8	13.5	16.0	
of species-environment relation	15.9	22.9	28.6	33.9	
Sum of all unconstrained eigenvalues					10.232
Sum of all canonical eigenvalues					4.831
					Significance of first canonical axis: F = 35.810, p <0.001
					Significance of all canonical axes: F = 5.647, p <0.001

The main gradient in plant community composition corresponded with a complete turnover from exotic-dominated communities in the pasture matrix (low pDCCA axis 1 scores) to native-dominated communities inside forest fragments (high pDCCA axis 1 scores) (see **Figure 2.2**). Axis 1 of the pDCCA was highly correlated with percent exotic richness (Pearson correlation, n = 516, r = -0.941, p <0.001, **Figure 2.3a**), and percent exotic cover in each plot (n = 516, r = -0.917, p <0.001, **Figure 2.3b**), confirming that the first pDCCA axis reflects the degree of exotic dominance in the plant community.

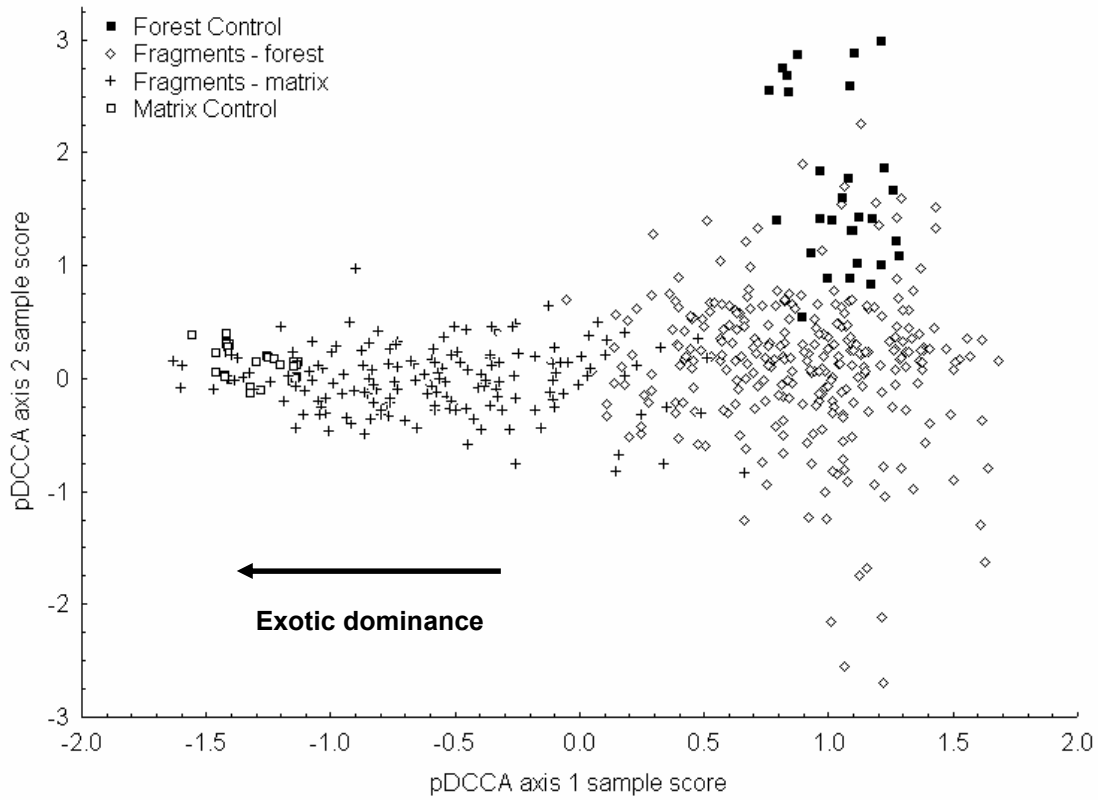


Figure 2.2. Partial detrended canonical correspondence analysis (pDCCA) of plant species composition (<2 m in height) in 516 plots. pDCCA axis 1 represents a turnover in plant species composition from a predominantly-exotic community in the matrix to a predominantly-native community in forest interior habitats. pDCCA axis 1 explained 7.5% of the variation in the species data, and axis 2 explained 3.3% of the variation. 70 environmental variables were entered in the pDCCA and the effects of three significant covariables (Altitude, Long, Long2Lat) were partialled out. Forest Control = deep forest interior plots in an un-fragmented landscape, Fragments - forest = plots inside forest fragments, Fragments - matrix = plots in matrix habitat next to fragments, Matrix Control = plots in matrix habitat in a heavily deforested landscape.

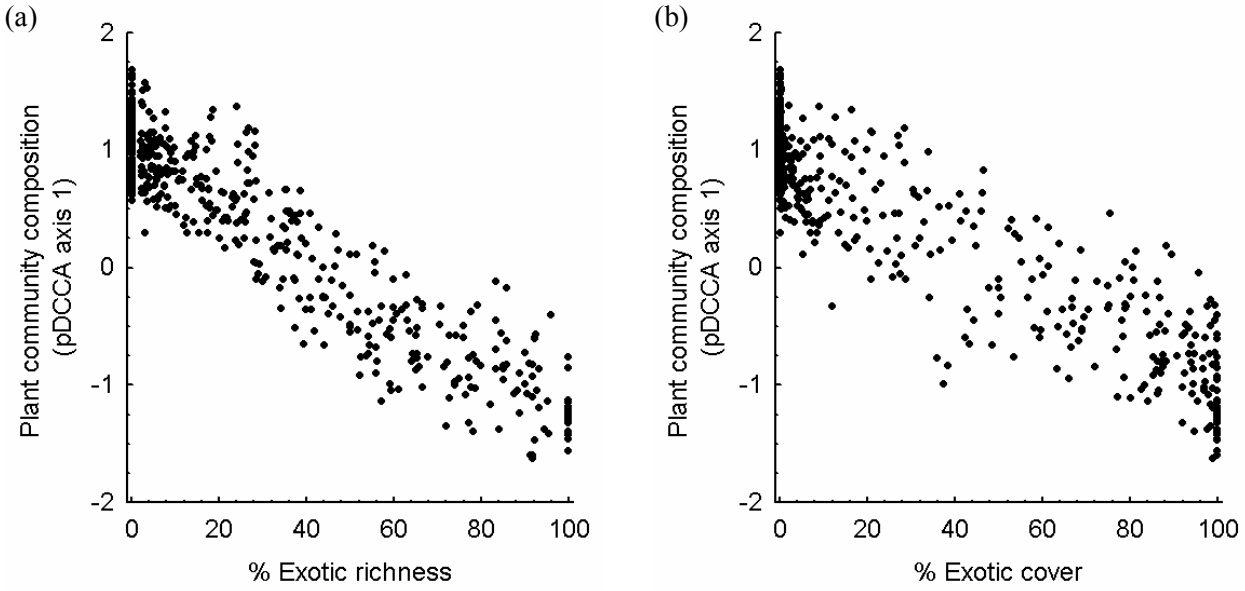


Figure 2.3. (a) Percent exotic richness and (b) percent exotic cover were highly correlated with axis 1 sample scores from a partial detrended canonical correspondence analysis (pDCCA) of plant community composition (<2 m in height) (n = 516, r = -0.941 and r = -0.917 respectively, p <0.001).

The marginal and conditional eigenvalues (**Table 2.4**) revealed that the dominant gradient in plant community composition was related to distance from the forest edge (Edgedist) (which explained 13.0% of the total variation in the plant species data) and percentage canopy cover (which explained 14.3% of the total variance). Canopy cover increased from the open matrix towards fragment interiors and was highly correlated with Edgedist ($r = -0.806$, $p < 0.001$, **Appendix 4**). The intra-set correlations confirmed that the first pDCCA axis represents an edge gradient in plant species composition, as Edgedist was highly correlated with axis 1 (see **Table 2.4**). MATdummy (Matrix Control dummy variable) also explained a large amount of the variation in species composition, as shown by its high marginal eigenvalue (explaining 9.1% of the total variance), and high correlation with axis 1 of the pDCCA (**Table 2.4**). This indicates that species composition at the Matrix Control sites was different from the other sites, and most likely reflects the position of the Matrix Controls at the extreme end of the edge gradient (see **Figure 2.2**).

Plant species composition was strongly related to a number of the fragment- and plot-level environmental variables (**Table 2.4**), and several of these variables were highly correlated with distance from the forest edge (see **Appendix 4**). For example, grazing intensity was highly correlated with pDCCA axis 1 ($r = -0.687$) and Edgedist ($r = 0.61$, $p < 0.001$), indicating that the plant community became less dominated by exotic species as grazing intensity declined from high grazing pressure in the pasture matrix to low intensity inside forest fragments. Sapling richness and density were also highly correlated with Edgedist, and had large correlations with pDCCA axis 1, reflecting the strong edge gradient in sapling richness and abundance. Of the macroclimatic and soil variables, only soil pH and soil carbon to nitrogen ratio (SoilCN) had important effects on plant species composition (**Table 2.4**). SoilpH was positively correlated with Edgedist ($r = 0.54$, $p < 0.001$), indicating that soils became more acidic inside forest fragments, whereas SoilCN decreased with Edgedist ($r = -0.60$, $p < 0.001$), meaning that soil nitrogen availability was higher near fragment edges. Community composition was strongly related to the cover of *Nothofagus fusca* (NOTfus) in the canopy and moss on the ground (**Table 2.4**), and these variables had high correlations with pDCCA axis 1, reflecting the fact that both NOTfus and moss cover increased inside fragments.

The treatment variables LogArea and Landscape had high positive correlations with pDCCA axis 1, indicating that the degree of exotic dominance in the plant community decreased with increasing fragment area and native forest cover in the landscape. LogArea and Landscape were highly correlated with a number of the environmental variables, including SoilCN ($r = 0.64$, $p < 0.001$), SoilpH ($r = -0.45$, $p < 0.001$), Drainage ($r = -0.48$, $p < 0.001$), and Tmin ($r = -0.60$, p

<0.001). These correlations revealed that soil nitrogen availability, soil pH, drainage, and the mean minimum temperature of the coldest month all decreased with increasing fragment area and forest cover in the landscape. The Landscape treatment was also highly positively correlated with NearBuil (distance to the nearest building, r = 0.72, p <0.001), and negatively correlated with Buil4096, Buil8192, Road2048 and Road4096 (see **Appendix 4**), indicating that the number of buildings and length of roads in the landscape decreased with increasing forest cover in the landscape.

Interestingly, three of the interaction variables, LscpEdge (landscape x edge distance interaction), LscpArea (landscape x fragment area interaction), and AreaEdge (fragment area x edge distance interaction), had stronger effects on plant species composition than the main effect of the Landscape treatment (**Table 2.4**). The LscpEdge interaction was the third most important treatment variable (explaining 8.9% of the total variance), with the third highest conditional eigenvalue and a high intra-set correlation with pDCCA axis 1 (r = -0.609, **Table 2.4**). The significant LscpEdge interaction means that edge effects on plant community composition varied in relation to the percentage of native forest cover in the landscape. Similarly, the significant AreaEdge interaction indicates that edge effects also varied with fragment size (see **Figures 2.4** and **2.5**). LxAxE also had a significant effect on plant species composition and was highly correlated with both the first two pDCCA axes, indicating that there was a complex three-way interaction effect between landscape, fragment area, and edge distance on plant species composition (see **Figure 2.6**).

FORdummy (Forest Control dummy variable) had the highest intra-set correlation with the second pDCCA axis (r = 0.366, **Table 2.4**), indicating that axis 2 mainly represents a difference in species composition between Forest Control sites and the other sites (see **Figure 2.2**). Fragment shape index had the second-highest correlation with axis 2 (r = 0.359), indicating that sites at the upper end of axis 2 had higher edge to interior ratios. This probably reflects the fact that larger areas of forest, such as the Forest Control sites, tend to have more complex shapes than smaller fragments (Pearson correlation between LogArea and ShapeInd, r = 0.89, p <0.001, **Appendix 4**).

A number of the landscape-level land cover variables (i.e. 512AX3, 256AX2 and 2048AX2) were important predictors of plant species composition (**Table 2.4**), suggesting that local plant communities were affected by land cover in the surrounding landscape at multiple spatial scales. The proportion of exotic grassland (pasture) in the landscape (ExoG) also appeared to be important, particularly at smaller spatial scales, as ExoG256, ExoG512 and ExoG1024 had high

correlations with axis 1. In contrast, other landscape-level variables were only influential at larger spatial scales e.g. the length of rivers in the landscape was most significant at the 4096 and 2048 m scales, with Riv4096 and Riv2048 being negatively correlated with pDCCA axis 1. Surprisingly, the number of buildings and length of roads in the landscape were not major predictors of plant species composition. The amount of native forest and shrubland in the landscape, number of native forest fragments, edge density, and connectivity between forest fragments also appeared to have relatively minor effects on plant community composition.

Table 2.4. Results of the forward selection procedure in pDCCA (partial detrended canonical correspondence analysis) to determine which environmental variables explained significant variation in plant species composition (<2 m in height) among 516 plots. A Monte Carlo procedure (999 random permutations) with a Bonferroni corrected p-value of 0.0003 was used to determine the significance of each variable. The effects of three significant covariables (Altitude, Long, Long2Lat) were partialled out. Marginal effects (i.e. independent effects) are shown for the 86 variables which had eigenvalues ≥0.10. Conditional effects (i.e. the additional effect of each variable after accounting for the effects of the other variables) are shown for the 70 variables which explained a significant amount of variation in the plant species data, and intra-set correlations between these variables and the first three pDCCA axes are shown. Correlations in bold are significant ($p < 0.0003$). λ = eigenvalue (fit) of each variable, λ_a = increase in eigenvalue (additional fit). Codes for variables are given in **Table 2.2**. Treatment variables are in bold.

Marginal effects		**Conditional effects**		**Intra-set correlations**		
Variable	**λ**	**Variable**	**λ_a**	**Axis 1**	**Axis 2**	**Axis 3**
Canopy	0.69	Canopy	0.69	**0.891**	0.047	0.023
Edgedist	0.63	**MATdummy**	0.34	**-0.450**	0.052	**0.169**
SaplingD	0.56	**LscpEdge**	0.18	**-0.609**	**-0.250**	-0.005
TreeDiv	0.53	NOTfus	0.16	**0.445**	**-0.265**	-0.089
MATdummy	0.44	**Edgedist**	0.14	**-0.851**	-0.093	0.038
Grazing	0.43	512AX3	0.12	-0.036	0.134	**-0.293**
LscpEdge	0.43	Riv4096	0.11	**-0.207**	**0.281**	0.020
SaplingN	0.35	Moss	0.10	**0.443**	**0.307**	-0.047
LiveTree	0.34	256AX2	0.10	**0.281**	-0.017	**-0.388**
SoilpH	0.34	2048AX2	0.09	**0.304**	-0.081	**-0.170**
AreaEdge	0.32	**FORdummy**	0.08	**0.187**	**0.366**	-0.020
Moss	0.30	8192AX3	0.08	-0.049	-0.147	0.074
Landscap	0.29	**LscpArea**	0.08	**0.295**	**0.242**	-0.088
NOTfus	0.28	**LogArea**	0.08	**0.365**	0.111	-0.156
ExoG256	0.25	SaplingD	0.07	**0.787**	0.090	-0.015
LxAxE	0.24	Buil256	0.07	0.023	-0.013	-0.061
NatF256	0.24	8192AX1	0.07	-0.025	**-0.222**	0.045
WEIrac	0.23	**AreaEdge**	0.07	**-0.428**	**-0.293**	0.000
SoilCN	0.23	Conn2048	0.07	0.086	-0.118	-0.131
LogArea	0.23	256AX3	0.06	**0.231**	-0.088	-0.045
LscpArea	0.22	NOTtru	0.06	**0.194**	**0.320**	-0.018
RaisedM	0.21	ExoG1024	0.06	**-0.278**	-0.013	0.108
ShapeInd	0.21	4096AX2	0.06	0.111	-0.109	0.021
SoilP	0.21	SaplingN	0.06	**0.565**	**0.188**	**-0.178**
256AX1	0.20	NND	0.06	0.115	**0.322**	0.050
FORdummy	0.20	**LxAxE**	0.06	**-0.292**	**-0.333**	0.015
256AX2	0.19	Edge1024	0.05	**0.207**	**-0.184**	**-0.356**
Edge2048	0.19	NatS4096	0.05	0.079	**0.295**	-0.001
256AX4	0.19	Road512	0.05	0.046	-0.113	**0.232**
ExoG512	0.18	ExoW4096	0.05	0.070	0.114	-0.059

Marginal effects		**Conditional effects**		**Intra-set correlations**		
Variable	**λ**	**Variable**	**λ_a**	**Axis 1**	**Axis 2**	**Axis 3**
NatF4096	0.18	Riv2048	0.05	**-0.283**	**0.255**	0.107
Edge1024	0.18	ShapeInd	0.05	**0.223**	**0.359**	-0.066
NOTtru	0.18	NOTmen	0.05	**0.312**	**-0.181**	0.068
2048AX2	0.17	4096AX3	0.04	-0.127	-0.069	0.109
Riv2048	0.17	512AX4	0.04	**0.285**	0.003	-0.098
NatF512	0.17	deer	0.04	0.061	-0.088	-0.102
NatF2048	0.16	Edge4096	0.05	0.058	0.052	-0.050
ExoG4096	0.16	NatS2048	0.04	-0.016	0.082	-0.049
dairy	0.16	Grazing	0.04	**-0.687**	0.018	-0.157
Riv4096	0.16	LDiv8192	0.04	-0.053	0.077	-0.025
QUIacu	0.16	**Landscap**	0.04	**0.428**	0.080	**-0.191**
4096AX4	0.16	Road4096	0.04	**-0.272**	**0.174**	-0.130
ExoG2048	0.16	QUIacu	0.04	**0.269**	0.048	-0.001
Road4096	0.15	LDiv2048	0.04	0.047	-0.016	-0.132
1024AX2	0.15	LENZ150	0.04	-0.005	**0.300**	-0.064
DACcup	0.15	beef	0.04	0.031	0.072	**-0.357**
NOTmen	0.15	JuneS	0.04	**0.134**	0.125	0.135
LDiv256	0.15	FNum1024	0.04	0.038	0.038	-0.076
NatF1024	0.15	2048AX4	0.04	**0.189**	-0.109	0.055
512AX1	0.15	DACcup	0.04	**0.280**	0.124	0.055
1024AX3	0.14	FNum4096	0.04	**-0.166**	0.088	0.016
NND	0.14	SoilCN	0.04	**0.346**	**0.205**	**-0.217**
2048AX3	0.14	Drainage	0.03	-0.124	**-0.261**	**0.220**
ExoG1024	0.14	ExoG256	0.04	**-0.411**	0.011	**0.192**
512AX4	0.14	Edge512	0.04	**0.143**	-0.148	**-0.284**
Drainage	0.13	Edge8192	0.03	-0.048	**0.205**	0.040
ExoW2048	0.13	ExoG8192	0.04	-0.123	**-0.266**	0.034
DACdac	0.13	Riv512	0.04	-0.136	-0.005	0.151
256AX3	0.13	Road256	0.04	0.012	-0.095	**0.194**
Conn1024	0.13	Riv1024	0.03	**-0.183**	0.108	0.071
512AX2	0.13	WEIrac	0.03	**0.423**	**0.166**	0.054
Road2048	0.13	RaisedM	0.03	**0.444**	0.039	-0.099
Buil2048	0.12	NearRiv	0.03	0.000	0.078	0.004
Edge256	0.12	LDiv512	0.03	0.102	-0.080	0.017
beef	0.12	LDiv256	0.03	0.109	-0.046	0.039
Edge512	0.12	1024AX3	0.03	**-0.273**	0.015	**0.163**
NearBuil	0.12	FNum2046	0.03	**-0.209**	0.145	-0.067
FNum2046	0.11	Buil1024	0.03	**-0.196**	0.037	0.040
ExoG8192	0.11	ExoW1024	0.03	0.113	0.055	-0.119
2048AX1	0.11	ExoG512	0.03	**-0.332**	-0.056	0.074
1024AX1	0.11					
Buil1024	0.11					
4096AX1	0.11					
2048AX4	0.11					
512AX3	0.11					
LENZ150	0.10					
NatS8192	0.10					
LDiv4096	0.10					
LENZ94	0.10					
ExoW4096	0.10					
FNum4096	0.10					
8192AX1	0.10					
NatS4096	0.10					
Riv1024	0.10					

2.3.2 Interactions between edge, area and landscape effects on community composition

The ordination results revealed that there were significant interaction effects between the edge, area and landscape treatments on plant community composition, and the parameters from the fitted edge response functions provide more detail about the nature of these interactions. Although the exact shape of the edge response varied to some degree among fragments, the logistic model was chosen as the best fit model for 41 out of 44 fragments (see **Appendix 5** for formulae of logistic functions and **Figure 2.4** for an example). The significance of the AreaEdge interaction indicates that edge responses in plant species composition varied in relation to fragment area. Plant communities in small fragments were more heavily invaded by exotic species than those in large fragments, and this difference was most apparent in the interior of forest fragments, as communities in fragment interiors (as measured by the β0 parameter from the logistic model) became more dominated by exotic species with decreasing fragment area (**Figure 2.5a**). In contrast, the slope of the edge gradient in plant community composition (as measured by the β3 parameter from the logistic model) was not related to fragment area, indicating that the steepness of the change in species composition along the edge gradient was similar for fragments of different sizes (**Figure 2.5b**).

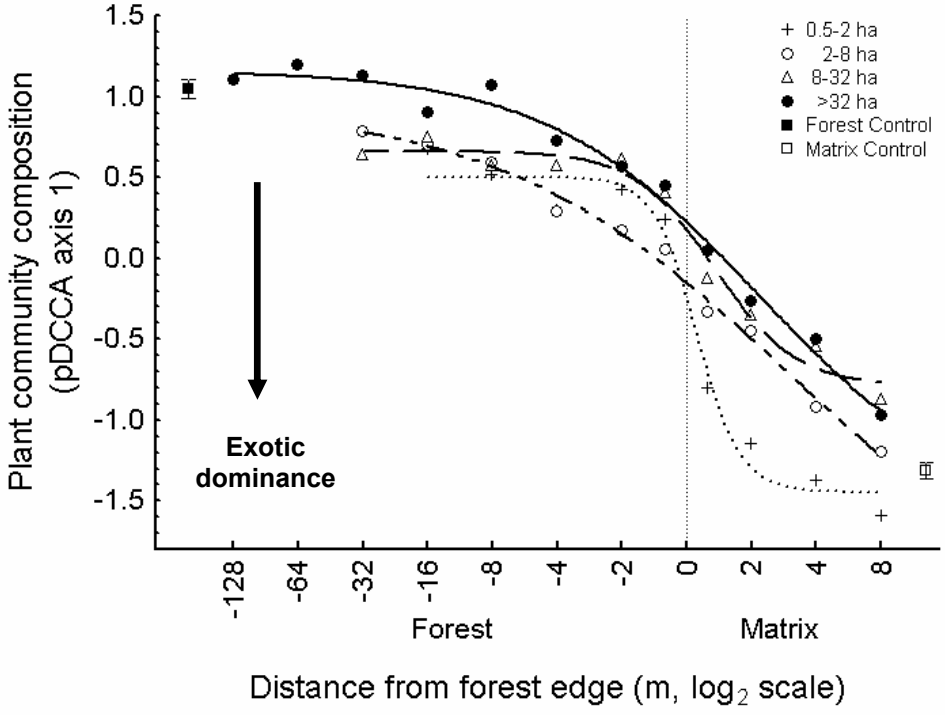


Figure 2.4. Representative example of edge gradients in plant community composition at forest fragments in four size classes (0.5-2.0 ha, 2.0-8.0 ha, 8.0-32.0 ha, >32.0 ha) in a landscape with 19.8% native forest cover. Landscapes were defined by circles with a 3 km radius. Plant community composition is represented by axis 1 sample scores from a partial detrended canonical correspondence analysis (pDCCA) of plant species composition (<2 m in height). Logistic functions were fitted to the observed data (see **Appendix 5** for formulae). Mean pDCCA axis 1 scores of Forest Control and Matrix Control plots are presented for comparison, but were not used in model fitting (error bars are ±95% confidence intervals).

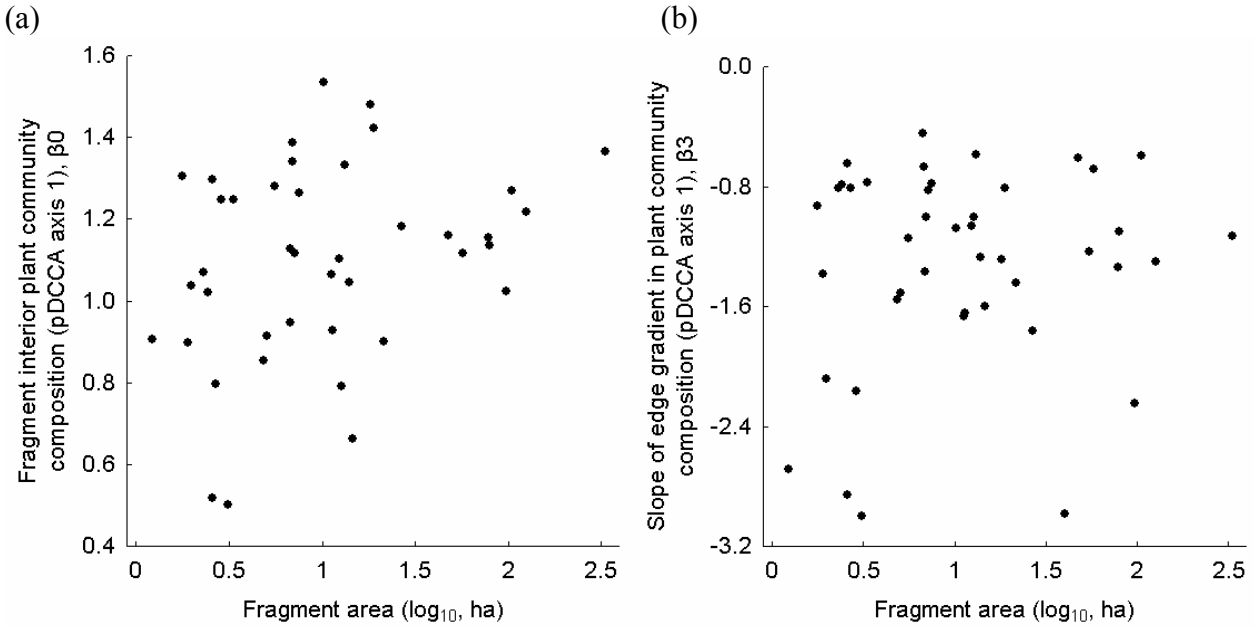
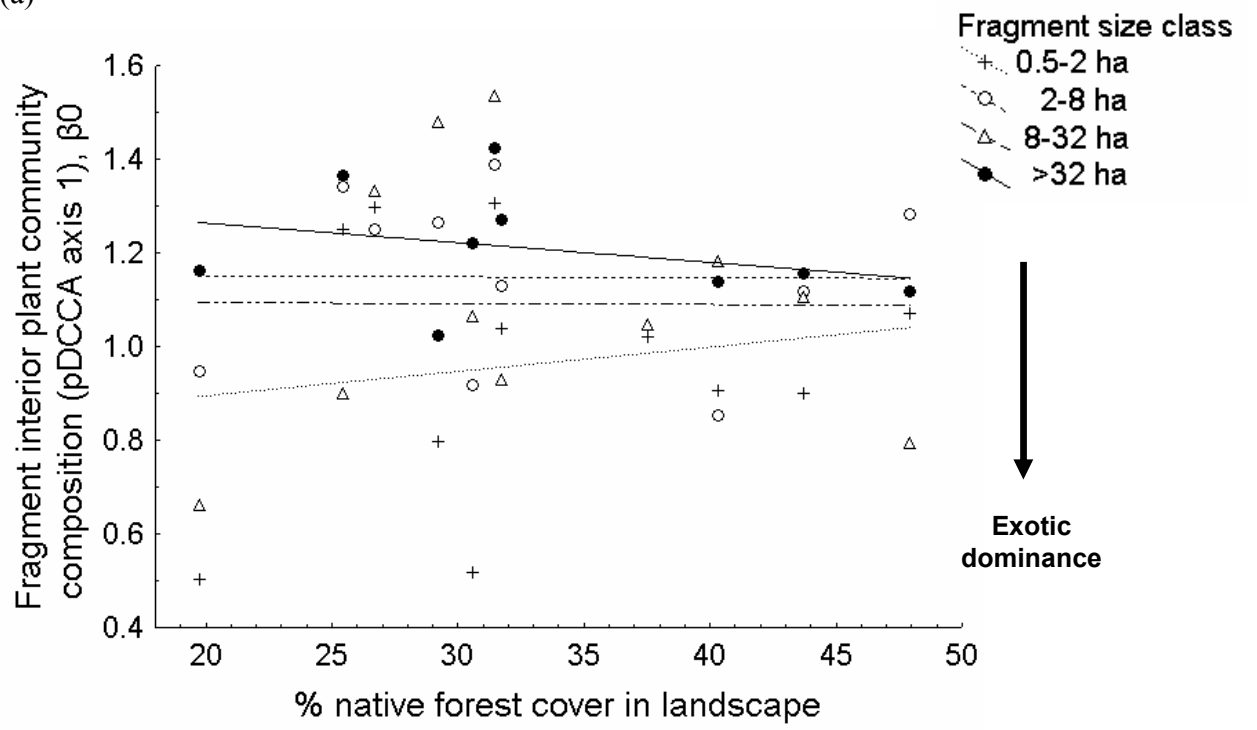


Figure 2.5. Fragment area versus (a) predicted fragment interior plant community composition (β0) and (b) the slope of the edge gradient in plant community composition (β3). Plant community composition is represented by axis 1 sample scores from a partial detrended canonical correspondence analysis (pDCCA) of plant species composition (<2 m in height). Values for β0 and β3 were calculated from logistic functions fitted to edge responses at each of the 41 fragments (see **Appendix 5** for formulae). Lower β0 values indicate greater dominance of exotic plant species in the community, and more negative β3 values indicate steeper changes in species composition along the edge gradient.

The ordination indicated that plant species composition was more strongly related to the LscpEdge and LscpArea interactions than the main effect of Landscape, indicating that edge and area effects on the plant community varied in relation to the amount of native forest cover in the landscape. The nature of these interactions is illustrated in **Figure 2.6a**, which shows the relationship between fragment interior species composition (β0) and the percentage of forest cover in the landscape for fragments in different size categories. We can see that the relationship between β0 and landscape forest cover changed from positive in very small fragments (<2 ha) to slightly negative in large fragments (>32 ha). This indicates that plant communities in very small fragments were more exotic-dominated in heavily deforested landscapes than in landscapes with a high percentage of native forest cover, whereas larger fragments showed no increase in exotic dominance with decreasing landscape forest cover. The slope of the edge gradient in plant species composition (β3) did not change consistently with fragment area or forest cover in the landscape, however the relationship with landscape cover did vary among different fragment size classes (**Figure 2.6b**). Very small fragments (<2 ha) showed a smaller change in species composition along the edge gradient in more intact landscapes than in more heavily deforested landscapes, whereas small fragments (2-8 ha) showed the opposite trend. Although landscape forest cover had an effect on β0 and β3, there was no apparent threshold in landscape forest cover (**Figure 2.6**).

(a)



(b)

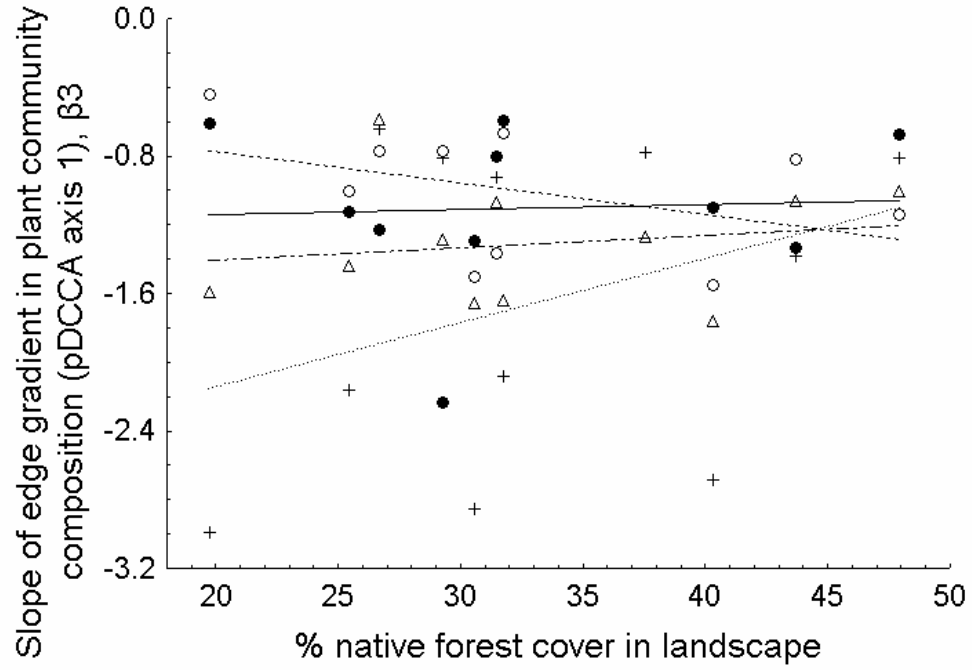


Figure 2.6. Edge effects on plant community composition in relation to fragment area and native forest cover in the landscape: (a) predicted fragment interior plant community composition (β0) and (b) slope of the edge gradient in plant community composition (β3). Fragments are shown in four size classes (0.5-2.0 ha, 2.0-8.0 ha, 8.0-32.0 ha, >32.0 ha). Plant community composition is represented by axis 1 sample scores from a partial detrended canonical correspondence analysis (pDCCA) of plant species composition (<2 m in height). Values for β0 (the first asymptote) and β3 (the slope of the edge gradient) were calculated from logistic functions fitted to edge responses at each of the 41 fragments (see **Appendix 5** for formulae). Lower β0 values indicate greater dominance of exotic species in the community, and more negative β3 values indicate steeper changes in species composition along the edge gradient. Percentage forest cover in each landscape was calculated within a circle with a 3 km radius centred on the four fragments in each landscape. A linear regression line has been fitted for each fragment size class.

2.3.3 Edge, area and landscape effects on percent exotic richness and percent exotic cover

The GLMs revealed that almost all of the treatment variables had significant effects on the degree of exotic invasion in the plant community, with mean percent exotic richness and mean percent exotic cover per plot being significantly related to landscape forest cover, fragment area, and distance from the forest edge (**Table 2.5**). Distance from the forest edge (Edgedist) had the strongest effect on the response variables, with exotic richness (**Figure 2.7a**) and exotic cover (**Figure 2.8a**) reaching up to 100% in the matrix, then declining to approximately 50% on average at the edge, and to 0% inside forest fragments. Fragment area (LogArea) had the second largest effect on the degree of exotic dominance, and this effect was negative, with percent exotic richness and cover increasing as fragment size decreased (**Figure 2.7b** and **Figure 2.8b**). Similarly, the proportion of native forest cover in the landscape had a significant negative effect on both exotic richness and cover, with exotic dominance increasing as the level of forest loss in the landscape increased (**Figure 2.7c** and **Figure 2.8c**).

Table 2.5. The effects of the treatment variables on mean percent exotic richness and mean percent exotic cover per plot, as determined by generalised linear models (GLMs) with Type I SS. The slope indicates whether the relationship was negative or positive. The effects of two confounding variables (Altitude and Aspect) were partialled out ahead of the treatment variables in the GLMs. N = 515 in all GLMs. Significance level: p <0.001***, p <0.01**, p <0.05*, NS = non-significant (p >0.05). See Methods for a description of the treatment variables.

	Percent exotic richness			Percent exotic cover		
Variable	**F**	**P**	**Slope**	**F**	**P**	**Slope**
Landscap	4.385	**0.037** *	−	7.467	**0.007** **	−
LogArea	65.770	**<0.001** ***	−	45.626	**<0.001** ***	−
Edgedist	1204.844	**<0.001** ***	+	1012.047	**<0.001** ***	+
LscpArea	8.159	**0.004** **	+	0.3605	NS	
LscpEdge	0.639	NS		5.200	**0.023** *	−
AreaEdge	37.935	**<0.001** ***	−	31.697	**<0.001** ***	−
LxAxE	3.619	0.058 NS	+	0.219	NS	

In addition to the main effects, interactions between the treatment variables also had significant effects on the dominance of exotic species in the community (**Table 2.5**). The interaction between edge and area effects (AreaEdge) was highly significant for both response variables, which suggests that the strength of the edge effect was dependent on fragment area. Landscape cover also appeared to influence the effects of the other treatment variables, as there was a significant landscape by area interaction (LscpArea) effect on percent exotic richness, and a significant landscape by edge interaction (LscpEdge) effect on percent exotic cover. The three-way interaction (LxAxE) was not significant for either response variable, although the effect was approaching significance for percent exotic richness ($F_{1,458} = 3.619$, $p = 0.058$).

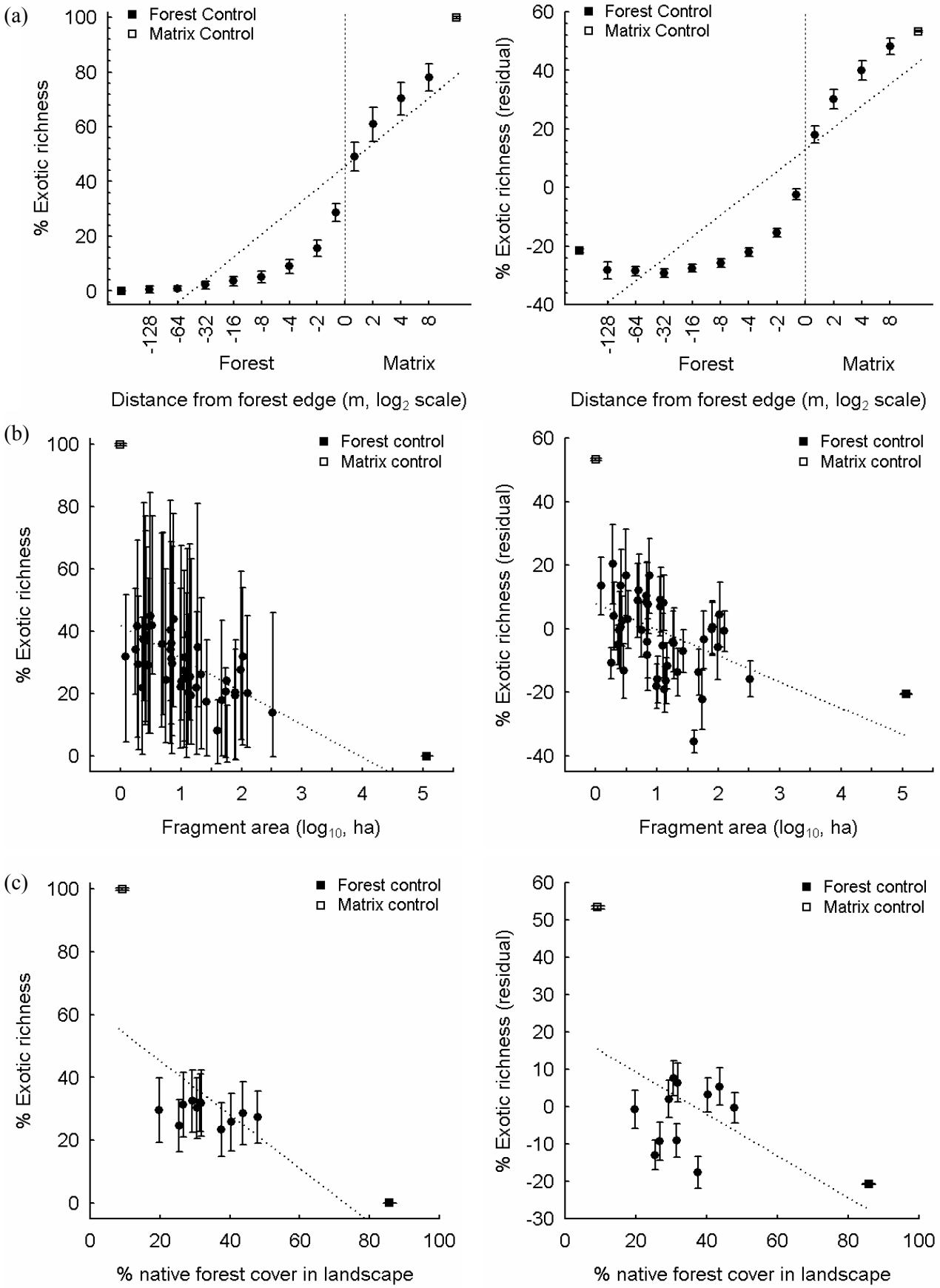


Figure 2.7. Mean percent exotic richness and mean residual percent exotic richness versus (a) distance from the forest edge, (b) fragment area, and (c) percent native forest cover in the landscape. Residual exotic richness was calculated after partialling out the effects of two confounding variables (Altitude and Aspect). Percent forest cover in each landscape was calculated within a circle with a 3 km radius centred on the four fragments in each landscape. Error bars show standard error. Linear regression lines are shown.

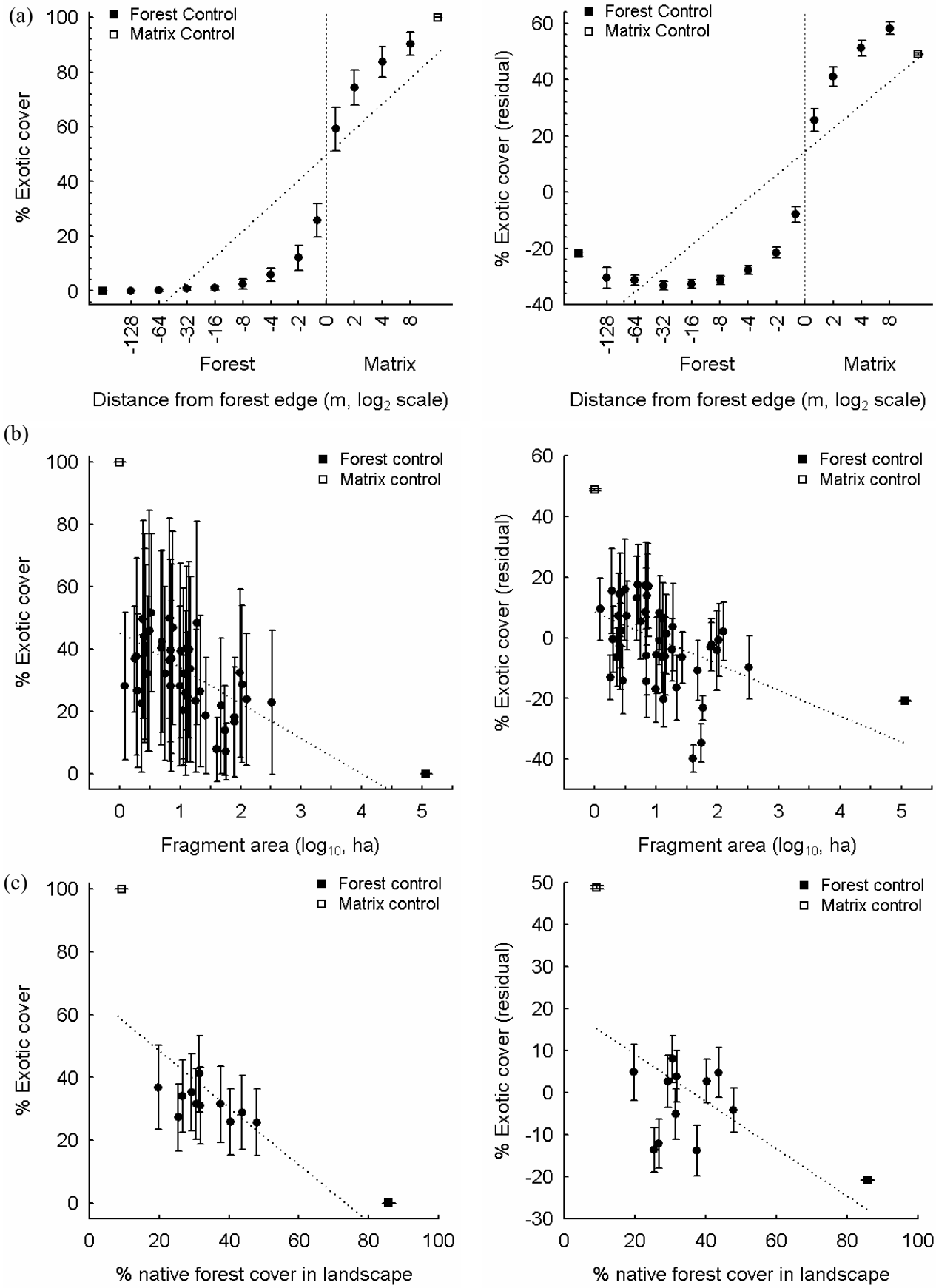


Figure 2.8. Mean percent exotic cover and mean residual percent exotic cover versus (a) distance from the forest edge, (b) fragment area, and (c) percent native forest cover in the landscape. Residual percent exotic cover was calculated after partialling out the effects of two confounding variables (Altitude and Aspect). Percent forest cover in each landscape was calculated within a circle with a 3 km radius centred on the four fragments in each landscape. Error bars show standard error. Linear regression lines are shown.

2.4 DISCUSSION

2.4.1 Edge and area effects on exotic plant invasions

Plant communities in forest fragments showed strong responses to fragmentation at multiple spatial scales, with significant edge, area, and landscape cover effects on plant species composition and the degree of exotic invasion in the community. As expected, distance from the forest edge had the strongest treatment effect on community composition, with exotic dominance decreasing inside fragments with increasing distance from the forest edge. Many previous studies have also found that the species richness, abundance, and growth of exotic plants were highest at the edges of forest fragments (Ranney *et al.* 1981; Brothers & Spingarn 1992; Fraver 1994; Luken & Goessling 1995; Burke & Nol 1998; Meiners & Pickett 1999; Cadenasso & Pickett 2001; Meekins & McCarthy 2001; Honnay *et al.* 2002; MacQuarrie & Lacroix 2003; Yates *et al.* 2004; Devlaeminck *et al.* 2005). In my study, distance from edge was highly correlated with light intensity (as estimated from forest canopy cover), which suggests that invasions of exotic plants into forest fragments may be limited by low light availability (Brothers & Spingarn 1992). This also implies that the majority of exotic plants recorded in my study are light-demanding, pioneer species that tend to occur in open matrix habitats (Burke & Nol 1998; Kupfer *et al.* 2006).

Fragment size also appeared to have a major influence on plant species composition, as communities in small fragments were more heavily invaded by exotic species than those in large fragments. Previous studies have also reported higher levels of exotic plant invasion (i.e. exotic richness and abundance or cover) in smaller fragments (Timmins & Williams 1991; Burke & Nol 1998; Harrison 1999; Kemper *et al.* 1999; Kumar *et al.* 2006; Ohlemüller *et al.* 2006). For example, a study in Otago, New Zealand revealed that species density of exotic plants decreased with forest fragment area (Ohlemüller *et al.* 2006), and a study in Canada found that exotic plant species penetrated more deeply into small woodlands than into large ones (Burke & Nol 1998). These trends are likely to arise because the effect of fragment area is usually inter-correlated with other factors driving plant invasion processes such as disturbance regime, soil characteristics, fragment age, and site history (past land use) (Ross *et al.* 2002; Aragón & Morales 2003; Lundgren *et al.* 2004; Ewers & Didham 2006a; Kupfer *et al.* 2006).

Grazing has previously been implicated in the facilitation of plant invasions into forest fragments, as it causes disturbance to understorey vegetation and soils, nutrient enrichment through faeces and urine, and stock may act as vectors for dispersal of plant propagules into fragments (Hobbs &

Huenneke 1992; Lozon & MacIsaac 1997; Abensperg-Traun *et al.* 1998; Duggin & Gentle 1998; Yates *et al.* 2000; Hobbs 2001; Vavra *et al.* 2007). In my study, grazing intensity decreased with distance into the forest and fragment area, and was associated with exotic dominance in the plant community, suggesting that grazing by stock may have promoted exotic plant invasions into forest fragments. Several other studies have also found that grazing intensity was higher in small forest fragments (Kemper *et al.* 1999; Hobbs 2001; Echeverría *et al.* 2007), and it seems likely that the impacts of grazing on plant communities may act synergistically with edge effects, further increasing rates of exotic invasions into forest fragments (Hobbs 2001; Vavra *et al.* 2007).

Soil characteristics also appeared to interact with the effects of fragmentation on plant community composition, as soil pH, soil nitrogen availability, and drainage were higher at edges, in small fragments, and in more heavily deforested landscapes. There are two potential explanations for these trends. Firstly, human agricultural activities such as the application of superphosphate fertilizer and soil drainage will result in elevated soil fertility and drainage levels in fragmented landscapes, and the influence of these activities is likely to be greatest at forest edges and in small fragments (McIntyre & Hobbs 1999). Secondly, the pattern of forest loss is not likely to be random, as the most productive parts of a landscape are usually modified first (Norton *et al.* 1995; Lindenmayer & Luck 2005). This means that more productive landscapes with higher fertility, better drainage, and less acidic soils are likely to experience a greater loss of forest cover than less productive landscapes, and fragments remaining in these landscapes will tend to be smaller and more modified. It seems likely that both of these processes have influenced plant communities in forest fragments in my study area, and that the effects of fragmentation have interacted with the underlying environmental characteristics to further promote plant invasions into fragments.

Few studies have examined two-way interactions between edge and area effects (Malcolm 1994; Didham *et al.* 1998; Barbosa & Marquet 2002; Ewers *et al.* 2007), however the results of these studies suggest that interactions among fragmentation effects may be relatively common. For example, a New Zealand study on beetles in forest fragments found significant interactions between fragment area and edge effects on species composition, as the strength of edge effects (measured by the slope of the edge gradient) increased in relation to fragment area (Ewers et al. 2007). In my study, plant communities in small fragments were more heavily invaded by exotic species than those in large fragments, however this difference was most apparent in the interior of forest fragments (rather than fragment edges), as communities in fragment interiors became more dominated by exotic species with decreasing fragment area. These results support the suggestion that small fragments may be more vulnerable to invasions because they have proportionally more

edge-affected habitat (Malcolm 1994), and are more affected by processes in the surrounding landscape that may promote invasions.

2.4.2 Landscape effects on exotic plant invasions

Recent research has revealed that landscape context can have a major influence on invasions in fragmented habitats (With 2002; Pauchard & Alaback 2004; Deckers *et al.* 2005; Gabriel *et al.* 2005; Bartuszevige *et al.* 2006; Henderson *et al.* 2006; Kumar *et al.* 2006; Duguay *et al.* 2007; Nesslage *et al.* 2007). For example, and a study in Rocky Mountain National Park, USA found that species richness of exotic plants increased with edge density in the landscape (landscapes ranged from 120 m to 960 m radius) (Kumar *et al.* 2006). Surprisingly few empirical studies have examined the effects of landscape forest cover on invasion processes, however two such studies have revealed that the amount of forest cover in the landscape was an important factor influencing plant invasions in forest fragments (Charbonneau & Fahrig 2004; Ohlemüller *et al.* 2006). The proportion of exotic plant species in forest sites in Ontario, Canada increased with increasing amount of open habitat in the surrounding landscape (within a 200 m radius) (Charbonneau & Fahrig 2004), and a study in New Zealand forest fragments found that species richness of exotic plants was higher in landscapes with low native forest cover (Ohlemüller et al. 2006). Similarly, I found that the proportion of native forest cover in the landscape had a significant effect on the richness and cover of exotic plants in the community, with exotic dominance increasing in landscapes with a higher degree of forest loss. The results suggest that the modified conditions in heavily deforested landscapes are more suitable for exotic species and that native fragments in these landscapes are more vulnerable to invasion by exotic plants.

Human population density and related infrastructure such as roads are often cited as important factors promoting exotic plant invasions in modified landscapes (Tyser & Worley 1992; Parendes & Jones 2000; Vilà & Pujadas 2001; Pyšek *et al.* 2002; Gelbard & Belnap 2003; Lundgren *et al.* 2004). For example, a study in New England, USA found that the species richness and cover of exotic plants in highland forests increased with greater human development, as measured by road size and the density of houses within 1 km (Lundgren *et al.* 2004). Roads facilitate plant invasions because they are associated with increased disturbances (e.g. increased dust, pollution and changes in microclimate), and act as corridors for movement of exotic plants by vehicles and animal dispersal vectors (Wace 1977; Spellerberg 1998). In my study, the number of buildings and length of roads in the landscape were higher in more heavily deforested landscapes, suggesting that land use intensity was higher in these landscapes. Surprisingly, these variables

were not strongly related to plant species composition in forest fragments, however, implying that these correlates of human modification and disturbance were not major drivers of plant invasions in my study area.

2.4.3 Interactions between edge, area and landscape effects

My analyses revealed significant interactions between edge, area and landscape effects on plant community composition, indicating that edge effects on the plant community varied in relation to fragment area and forest cover in the landscape. Interestingly, the interaction effects on community composition were stronger than the main effects of landscape cover or fragment area, and this suggests that ignoring interaction effects could confound the detection of species responses to habitat fragmentation (Ewers & Didham 2006a). In very small fragments (<2 ha in size), interior plant communities were more heavily invaded by exotic species in severely deforested landscapes than in landscapes with high native forest cover. In contrast, larger fragments showed no obvious trend, with exotic dominance being unrelated to native forest cover in the landscape. The results agree with my prediction that plant communities in small fragments would be affected by the loss of forest cover in the landscape more than large fragments. The combined effects of small fragment size and low forest cover in the landscape appear to make very small fragments highly vulnerable to invasion by exotic plants. It is difficult to compare my results with previous research, as no other studies have examined multiple interactions between edge, area, and landscape effects simultaneously, nor have these effects been examined in relation to invasion processes. My results confirm the importance of testing for multiple interactions in fragmentation studies, as failing to do so could result in underestimation of the impacts of fragmentation on species occupying very small fragments in heavily deforested landscapes.

The existence of landscape thresholds on ecological responses has been demonstrated by a number of studies (Villard *et al.* 1999; Bascompte & Rodríguez 2001; Radford & Bennett 2004; Radford *et al.* 2005; Dodd *et al.* 2006; Betts *et al.* 2007), however exotic plant invasions in native forest fragments did not appear to respond to a threshold in landscape forest cover in my study. Similarly, a recent study in Australia found no evidence for threshold effects of vegetation cover on bird or reptile assemblages (Lindenmayer *et al.* 2005). It is possible that a threshold was not apparent in my study because the landscapes contained >20% forest cover, meaning that they may have all been above the threshold level of forest cover. In addition, the spatial scale of my landscape treatment variable (3 km radius) may not have been appropriate for the entire plant community, as individual species will respond differently to spatial scale (Turner 1989; Withers &

Meentemeyer 1999; Huggett 2005). Another explanation is that deforestation has occurred relatively recently in my study area on the West Coast, and is still ongoing, meaning that there is a weak relationship between current landscape cover and species' distributions (Wiser *et al.* 1998). In this situation, the distribution and abundance of exotic plants is unlikely to be at equilibrium with the current landscape structure, resulting in an "invasion debt" (Seabloom *et al.* 2006). This concept is analogous to that of the 'extinction debt' (Tilman *et al.* 1994; Hanski & Ovaskainen 2002; Vellend *et al.* 2006), meaning that in my study area, invasions into forest fragments are predicted to increase over time as populations of invasive species expand throughout fragmented landscapes (Seabloom *et al.* 2006).

Chapter 3 – Linking plant species traits to their invasiveness in native forest fragments

3.1 INTRODUCTION

Invasive plants have major social, economic and environmental impacts, and there is an urgent need to understand the factors determining the invasiveness of exotic plants, so that we can better manage their spread (Mack *et al.* 2000; Mooney & Hobbs 2000; Kolar & Lodge 2001; Henderson *et al.* 2006). Many studies have explored the role of exotic species traits in influencing their invasiveness, and a number of characteristics of successful plant invaders have been suggested (Noble 1989; Roy 1990; Rejmanek 1996; Rejmánek & Richardson 1996; Williamson & Fitter 1996b; Daehler 1998; Goodwin *et al.* 1999; Bellingham *et al.* 2004; Hamilton *et al.* 2005; Buckley *et al.* 2006; Thuiller *et al.* 2006; Aronson *et al.* 2007; Thompson & McCarthy 2008). These characteristics include: short juvenile period, high seed output, rapid growth, vegetative reproduction, long-distance dispersal, large specific leaf area, and long flowering period (Baker 1965; Rejmánek & Richardson 1996; Williamson & Fitter 1996b; Daehler 2003; Hayes & Barry 2008). Despite the appeal of developing a suite of traits to predict which species will become invasive when introduced to a new region, the definition of an ideal invader has proven to be problematic (Thompson *et al.* 2001; Hayes & Barry 2008; Moles *et al.* 2008; Whitney & Gabler 2008). The importance of particular traits in contributing to invasion success is inevitably context dependent and will vary according to the habitat or community encountered or the stage of invasion (Thompson *et al.* 1997; Alpert *et al.* 2000; Kolar & Lodge 2001; Lake & Leishman 2004; Lloret *et al.* 2005; Facon *et al.* 2006; Richardson & Pysek 2006).

Traits commonly used to predict invasiveness include both intrinsic life history traits, such as seed size or life form, and attributes relating to their interaction with humans, such as the reason for introduction to a country (Goodwin *et al.* 1999; Hamilton *et al.* 2005). Life form (or growth form) appears to contribute to invasiveness in some studies, although results vary among different habitats (Lodge 1993; Alpert *et al.* 2000; Lake & Leishman 2004; Thuiller *et al.* 2006; Aronson *et al.* 2007; Herron *et al.* 2007; Thompson & McCarthy 2008). For example, a study in Australia found that the main invaders in physically disturbed sites were small herbs and grasses, whereas in sites subject to water and nutrient enrichment, exotic species were more likely to be climbers and species with vegetative propagation (Lake & Leishman 2004).

The type of dispersal mechanism/s utilised by a plant species could also influence their invasiveness, as this will affect their ability to move around in the landscape and thus take advantage of new habitats (Rejmanek 1996; Kolar & Lodge 2001; Lake & Leishman 2004; Lloret *et al.* 2005; Buckley *et al.* 2006). For example, plants with abiotic dispersal mechanisms (e.g. anemochory, hydrochory) could have higher dispersal rates in deforested landscapes compared to species dispersed by animals because of elevated wind speeds in open habitats and reduced populations of animal mutualists (McEuen & Curran 2004).

The life span or longevity of plants could also influence their invasiveness (Lodge 1993). Species with short life cycles (i.e. annuals and biennials) reproduce rapidly, enabling them to spread and expand their populations in a short time (Grime 1979). This strategy is likely to be most advantageous in relatively open, disturbed habitats (Thompson *et al.* 1997; Lake & Leishman 2004). In contrast, long-lived perennials may not reproduce for a number of years, so their initial rate of spread may be slower, but they are likely to compete more strongly and have greater impacts on native communities in the long-term through their ability to persist and alter ecosystem processes (Vitousek & Walker 1989; Standish *et al.* 2004). For example, a study on the traits of invasive plants in Europe found that invaders were most likely to be polycarpic perennials with clonal growth and erect, leafy stems, especially in relatively undisturbed communities in cool, damp climates (Thompson *et al.* 1997).

Geographic range and habitat breadth have been associated with plant invasiveness and are thought to influence their ability to invade new habitats (Scott & Panetta 1993; Goodwin *et al.* 1999; Dehnen-Schmutz *et al.* 2007b; Milbau & Stout 2008; Ricklefs *et al.* 2008). Species that are widely distributed in their native range are likely to be able to spread widely outside their region of origin because they can tolerate broad environmental conditions (Goodwin *et al.* 1999; Williams & Wiser 2004). Not surprisingly, being invasive in one location is known to be one of the best predictors of invasiveness in similar environments elsewhere (Scott & Panetta 1993; Reichard & Hamilton 1997; Herron *et al.* 2007; Milbau & Stout 2008). A range of plant physiological traits such as drought, temperature, and shade tolerance will also have a major influence on their ability to invade particular habitats (Maule *et al.* 1995; Fine 2002), however these attributes are difficult to measure, hence this information is unavailable for many species.

Human interaction with plants has a major role to play in invasions, as human activities such as agriculture, horticulture and gardening lead to both deliberate and accidental spread of species throughout the globe (Heywood 1989; Mack 1996; Mack & Lonsdale 2001; Reichard & White

2001; Taylor & Irwin 2004; Křivánek *et al.* 2006; Williams & Cameron 2006; Dehnen-Schmutz *et al.* 2007b; Caley *et al.* 2008). The reason for the initial introduction to a country (introduction mode) and human uses of plants will influence their propagule pressure and hence their probability of naturalisation and invasion (Esler 1987; Sullivan *et al.* 2004; Sullivan *et al.* 2005; Křivánek *et al.* 2006; Lambdon & Hulme 2006; Gravuer *et al.* 2008; Lambdon 2008; Milbau & Stout 2008). The year of introduction is also important for determining species' invasiveness, as the probability of naturalisation (and subsequent invasive spread) increases with time since introduction (or residence time) (Scott & Panetta 1993; Mulvaney 2001; Castro *et al.* 2005; Cadotte *et al.* 2006; Guo *et al.* 2006; Dehnen-Schmutz *et al.* 2007b; Caley *et al.* 2008).

The New Zealand native vascular flora (which comprises approximately 2400 species) is dwarfed by the number of exotic species, with over 24,000 species being introduced to New Zealand since human colonization (Williams & West 2000). Over 10% of exotic species have subsequently naturalised (Williams & West 2000), and the overall rate of naturalisation has grown since European colonization (Gatehouse 2008). The Department of Conservation currently lists over 320 exotic species as environmental weeds (Howell 2008), and most of these originate from the Northern Hemisphere (Williams & West 2000). Three quarters of environmental weeds were deliberately introduced to New Zealand as ornamental plants, 14% were originally introduced for agriculture, horticulture or forestry, and only 10% were accidental introductions (Buddenhagen *et al.* 1998; Howell 2008). Environmental weeds are considered to be major threats to New Zealand's native ecosystems (Owen 1998; Williams & West 2000), and understanding weed impacts and the factors driving exotic plant invasions is essential for conservation and management of native biodiversity (Atkinson & Cameron 1993; Clout & Lowe 2000).

The invasiveness of exotic plants in New Zealand is likely to be influenced by both intrinsic life history traits and the history, distribution and weed status of the species in New Zealand. The objective of my study was to examine the role of exotic plant traits in determining their invasiveness in fragmented native forests on the West Coast of New Zealand, and to assess whether different traits promote invasiveness in two different habitats: edges of forest fragments versus forest interior habitats. Based on the findings of previous studies (Scott & Panetta 1993; Goodwin *et al.* 1999), I expected that species which have been naturalised in New Zealand for a long time and are widely distributed throughout the country are likely to be widespread on the West Coast and be common at fragment edges. I also predicted that perennials will have been more successful at invading the interiors of forest fragments than short-lived species (annuals and biennials) because of their ability to persist over time in native forest communities. Shade

tolerance can have a major influence on invasiveness in forest habitats (Hutchinson & Vankat 1997a; Martin & Marks 2006), and I predicted that species with high shade tolerance would be more successful at invading forest interior habitats than those with low tolerance of shade. In addition, species listed as environmental weeds by the Department of Conservation were expected to be more invasive than other exotic plant species, particularly in forest interior habitats.

3.2 METHODS

3.2.1 Study area

The study was carried out in the Grey and Buller Districts on the West Coast of the South Island of New Zealand (42°08' to 42°36' and 171°25' to 171°46'). See **Chapter 2, section 2.2.1** for a full description of the study area, and **Figure 2.1** for a map.

3.2.2 Landscape and fragment selection

The study was conducted in 44 native forest fragments, which ranged in size from 0.3 to 330 ha. A geographic information system (GIS) analysis of the New Zealand Land Cover database (MfE 2004) was used to select 11 landscapes which ranged in native forest cover from 19.8% to 47.9%. Within each landscape, one native forest fragment was selected in each of four different size categories: 0.5-2.0 ha, 2.0-8.0 ha, 8.0-32.0 ha and >32.0 ha (see **Table 2.1** for a list of landscapes and fragments). See **Chapter 2, section 2.2.2** for a full description of the methods used to select landscapes and fragments. Note that data from the two Control landscapes (Forest Control and Matrix Control) were not used in this chapter because I wanted to focus on the invasion of exotic species in native forest fragments.

3.2.3 Selection of edge gradients

See **Chapter 2, section 2.2.3** for a full description of the methods used to select the edge gradient sampled at each forest fragment and **Table 2.1** for the length of edge gradient at each fragment.

3.2.4 Plant traits

Nine traits were recorded for each exotic plant species (see **Table 3.1**). These traits were chosen because they were expected to influence the abundance of naturalised plants in the study area and

their ability to invade native forest fragments (Rejmánek & Richardson 1996; Goodwin *et al.* 1999), and data for these traits were readily available in New Zealand. Trait character states were determined using information from the literature (Healy & Edgar 1980; Fitter *et al.* 1984; Webb *et al.* 1988; Edgar *et al.* 2000; Heenan *et al.* 2002; Howell 2008), the Landcare Research Ecotraits online database (Landcare Research 2008), and a database of traits for the entire naturalised flora of New Zealand (Gatehouse 2008).

Five of the traits are considered to be life history traits that are intrinsic to each species: life form, duration, dispersal mechanism, shade tolerance and the length of the flowering period (**Table 3.1**). (1) Species were categorised into six different life forms: ferns, grasses, herbaceous dicotyledons, rushes/sedges, shrubs/lianes, and trees. Rushes and sedges (Cyperaceae and Juncaceae) were combined into one group for analysis, and woody lianes were grouped with shrubs. Species from the Iridaceae family were grouped with grasses (Poaceae). (2) The duration (or longevity) of each species was described as annual, biennial or perennial. (3) One or more types of dispersal mechanism were assigned to each species: animal (endozoochory), attachment (exozoochory), ballistic, water (hydrochory), wind (anemochory), and unspecialised. (4) The degree of shade tolerance was categorised as low, moderate or high. (5) The average length of the flowering period in each year (in months) was determined for each species.

The four remaining traits reflect the history, distribution and status of each species in New Zealand. (6) The reason for the introduction of the species to New Zealand (introduction mode) was categorised as accidental, ornamental or utility. Ornamental species are those that were deliberately introduced to New Zealand and planted for ornamental purposes, whereas utility plants are those deliberately introduced for agriculture, horticulture or forestry. Accidental introductions comprise species that are known to have arrived in New Zealand as contaminants of imported goods such as seed, wool, packaging materials and so on. (7) The year of naturalisation in New Zealand is the earliest year that each species was recorded as being naturalised in New Zealand. (8) New Zealand was divided into 10 regions – Auckland/Northland, Waikato, East Coast, Taranaki, Wellington, Tasman, Canterbury, Westland, Otago, Southland – and the number of regions occupied by each species was determined (Healy & Edgar 1980; Webb *et al.* 1988; Heenan *et al.* 2002; Gatehouse 2008). (9) The conservation weed status of each species was determined from a recent list of environmental weeds in New Zealand (Howell 2008).

Table 3.1. Traits assigned to exotic plant species in this study and the number of species recorded in each category. Length of flowering period, year naturalised in New Zealand and the number of regions occupied in New Zealand were analysed as continuous variables, but are grouped into categories in this table for display purposes.

Species trait	Categories (Units)	No. of species	Data source/s
Life form	Fern	1	Healy & Edgar (1980)
	Grass	12	Webb *et al.* (1998)
	Herbaceous dicot	64	Edgar *et al.* (2000)
	Rush/sedge	12	Heenan *et al.* (2002)
	Shrub/liane	8	
	Tree	6	
Duration	Annual	14	Webb *et al.* (1998)
	Biennial	10	Edgar *et al.* (2000)
	Perennial	79	
Dispersal mechanism	Animal (endozoochory)	27	Landcare Research (2008)
	Attachment (exozoochory)	21	Gatehouse (2008)
	Ballistic	7	
	Water (hydrochory)	21	
	Wind (anemochory)	45	
	Unspecialised	17	
Shade tolerance	Low	73	Fitter *et al.* (1984)
	Medium	24	Landcare Research (2008)
	High	6	
Length of flowering period (months)	1-3	23	Fitter *et al.* (1984)
	4-6	39	Webb *et al.* (1998)
	7-9	22	Landcare Research (2008)
	10-12	19	
Introduction mode in New Zealand	Accidental	64	Gatehouse (2008)
	Ornamental	18	
	Utility	21	
Year naturalised in New Zealand	1800-1850	10	Webb *et al.* (1998)
	1851-1900	65	Gatehouse (2008)
	1901-1950	22	
	1950-2000	6	
Number of regions occupied in New Zealand	1	1	Healy & Edgar (1980)
	2	0	Webb *et al.* (1998)
	3	2	Edgar *et al.* (2000)
	4	2	Heenan *et al.* (2002)
	5	3	Gatehouse (2008)
	6	4	
	7	7	
	8	3	
	9	6	
	10	75	
Environmental weed status in New Zealand	No	72	Howell (2008)
	Yes	31	

3.2.5 Statistical analyses

Generalised linear models (GLMs) were used to examine the relationships between species traits and their invasiveness in native forest fragments. Two response variables were calculated for each species: (1) the proportion of edge plots invaded per fragment (out of 6 plots per fragment), and (2) presence in the interior of each fragment (coded as 1 if present, or 0 if absent in plots at edge distances -16 to -128 m inside fragments). The first response variable – the proportion of edge plots invaded per fragment – was calculated along a standardised edge gradient from 8 m inside fragments (-8, -4, -2 and -0.33 m edge distances) to 2 m in the matrix (+0.33 and +2 m edge distances) because the length of edge gradient sampled varied among fragments. The goal in this analysis was to determine which traits affect the invasion of exotic plants at fragment edges, while the second response variable was used to test whether a different set of traits affect invasion into forest interior habitats.

Two treatment variables, native forest cover in the landscape and fragment area, were included first in the GLMs, in order to partial out their potential confounding effects on the response variables and allow the effects of species traits to be examined independently from broader fragment and landscape factors. Landscape cover was defined by the percentage of native forest cover within a 3 km radius circle centred on the four fragments in each landscape, and fragment area was $\log_{10}$ transformed. The percent cover of each exotic species in the matrix adjacent to each fragment (i.e. average of +8, +4, +2, and +0.33 edge distances) was included as a predictor in the GLM for the second response variable, in order to partial out the effect of local propagule pressure on presence in the interior of each fragment.

The six dispersal mechanisms were entered as separate binary variables because some species had more than one dispersal mechanism. The GLM for the first response variable (proportion of edge plots invaded per fragment) was tested using a logit link function and a quasibinomial distribution because the data were proportions and over-dispersion was detected in the data. The GLM for the second response variable (presence in fragment interiors) was tested using a logit link function and a binomial distribution because the data were binary (presence/absence). The effect of each plant trait on the response variables was assessed in two ways: (1) χ^2 and *P* values from Type I (sequential) sums of squares (SS), and (2) χ^2 and *P* values from Type III SS, which indicates the additional effect of each trait after accounting for the effects of the other plant traits. Planned comparisons using orthogonal *a priori* contrasts were also included in the GLMs in order to

determine whether there were significant differences between particular categories of categorical traits. Trait categories that were expected to have contrasting effects on the response variables were compared in the contrasts. The contrasts were:

(a) life form:

- woody (tree and shrub) versus non-woody (fern, herb, grass and rush/sedge)
- fern versus other non-woody (herb, grass and rush/sedge)
- herb versus grass and rush/sedge
- grass versus rush/sedge
- tree versus shrub

(b) duration:

- short-lived (annual and biennial) versus perennial
- annual versus biennial

(c) introduction mode:

- accidental versus deliberate (ornamental and utility)
- ornamental versus utility

(d) shade tolerance:

- low versus moderate and high
- moderate versus high

Only one species of fern was recorded, so GLMs with the fern category removed were also tested, in order to determine whether the life form effect was significant without this category. R version 2.4.1 was used for all statistical analyses (R Development Core Team, 2006).

3.3 RESULTS

3.3.1 Characteristics of exotic plant species in this study

A total of 103 exotic species from 29 plant families were recorded at native forest fragments (see **Appendix 3** for a list of species). Herbaceous dicotyledons were the most common life form (62.1% of species), followed by rushes and sedges (11.7% of species), and grasses (11 species of grass and one iris) (see **Table 3.1**). Eleven woody species (trees, shrubs and lianes) and one fern species (*Dryopteris dilatata*) were recorded. The shrub group included three species of scramblers/lianes – *Rubus fruticosus*, *R. laciniatus* and *Hedera helix*. The majority of species were perennials (76.7%). Abiotic dispersal mechanisms were more widespread than biotic mechanisms (73 species versus 48 species), and 17 species had no specialised dispersal mechanism. Wind was

the most common means of dispersal (32.6% of species), followed by animal (endozoochory, 19.6%), attachment (exozoochory) and wind (15.2% each). Most species had low shade tolerance (70.9% of species), 24 species (23.3%) had moderate shade tolerance, and only 6 species were considered to have a high tolerance of shade. The length of flowering period varied widely among species, however 60.2% of species had flowers for six months or less per year.

Nearly two-thirds (62.1%) of the species were accidentally introduced to New Zealand, with fewer species being introduced for agricultural (20.4%) or ornamental purposes (17.5%). The year of naturalisation in New Zealand ranged from 1827 to 1983, with the majority of species (72.8%) becoming naturalised before 1900, and only six species after 1950. Almost one third of species were listed as environmental weeds in New Zealand, and nearly three-quarters (75 species) were present in all 10 mainland regions of New Zealand, indicating that most species recorded in this study were widely distributed throughout the country.

Five species were present at nearly all of the study sites – *Holcus lanatus, Lotus pedunculatus* (present at 43 out of 44 fragments), *Anthoxanthum odoratum, Ranunculus repens* (42 fragments), and *Hypochaeris radicata* (41 fragments), however the mean number of fragments invaded per species was only 8.8 ±1.6, and almost 30% of species occurred at only one fragment. The majority of species (approximately 70%) were not recorded in fragment interiors (≥16 m inside fragments), however three species – *Geranium robertianum*, *Hedera helix* and *Ilex aquifolium* – were only recorded ≥16 m inside fragments, although each occurred in only one fragment. The most successful forest invader was *Mycelis muralis*, a perennial dicot herb, which had invaded 13 fragment interiors (i.e. 29.5% of fragments).

3.3.2 The effects of plant traits on the proportion of plots invaded at fragment edges

In the GLM analyses, the landscape treatment variable had no effect on the mean proportion of edge plots invaded per fragment (**Table 3.2**). In contrast, fragment area had a highly significant effect, with the proportion of edge plots invaded decreasing with fragment area (**Table 3.2**). After accounting for the effects of landscape context and fragment area, almost all of the plant traits had significant effects on the proportion of edge plots invaded per fragment (**Table 3.2**). Introduction mode had the largest Type I effect ($\chi^2 = 610.4$, $p < 0.001$) and the second largest Type III effect ($\chi^2 = 91.5$, $p < 0.001$) on the response variable, with species that were deliberately introduced for agriculture or horticulture (utility species) having invaded significantly more edge plots than

accidental or ornamental introductions (*a priori* contrast, p <0.001) (**Figure 3.1a**). Life form had large Type I and Type III effects on the proportion of edge plots invaded per fragment (**Table 3.2**), with grasses, shrubs/lianes and ferns invading the highest number of edge plots, while trees invaded very few edge plots (**Figure 3.1b**). Planned comparisons using *a priori* contrasts revealed that woody species (trees and shrubs) had invaded significantly fewer plots than non-woody species (*a priori* contrast, p <0.001), grasses had invaded significantly more edge plots than rushes and sedges (*a priori* contrast, p <0.001), and trees had invaded significantly fewer edge plots than shrubs (*a priori* contrast, p <0.001). The effect of life form remained highly significant with the fern category removed from the data (Type I SS, $\chi^2 = 351.8$, p <0.001 and Type III SS, $\chi^2 = 99.2$, p <0.001).

Duration (longevity) had a highly significant effect on the mean proportion of edge plots invaded per fragment (**Table 3.2**), with perennials invading significantly more plots than shorter-lived species (annuals and biennials) (*a priori* contrast, p <0.001, **Figure 3.1c**). The degree of shade tolerance also had a significant influence on the proportion of plots invaded at fragment edges; this effect was strongest with the other plant traits included in the model (Type III SS, $\chi^2 = 54.4$, p <0.001) (**Table 3.2**). Species with low shade tolerance have invaded a significantly higher proportion of plots at fragment edges than species with moderate to high tolerance of shade (*a priori* contrast, p <0.001, **Figure 3.1d**). The average length of the flowering period had no significant effect on the response variable (**Table 3.2**).

Dispersal mechanism appeared to have a strong influence on the proportion of edge plots invaded, as almost all of the dispersal modes had significant effects in the model (only unspecialised dispersal showed no effect, **Table 3.2**). Species dispersed by animals (endozoochory and exozoochory) have invaded significantly fewer edge plots per fragment than species lacking these dispersal mechanisms (**Figure 3.1g, h**), while species with ballistic and wind dispersal have invaded significantly more edge plots than those without (**Figure 3.1i,j**). The effect of water dispersal was only significant after all the other traits were included in the model (Type III SS, $\chi^2 = 18.9$, p <0.001, **Figure 3.1k**).

Table 3.2. The effects of species' traits on the proportion of edge plots invaded per fragment by exotic plants after accounting for the effects of landscape context and fragment area (from 2 m in the matrix to -8 m into fragments). χ^2 values from Type I and Type III sums of squares from GLMs tested with quasibinomial distributions are shown. Landscape context was defined by the percentage of native forest cover within a 3 km radius. Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*, NS = non-significant (p >0.05). See Methods for definitions of trait categories.

Predictors	Model estimate		GLM with Type I SS		GLM with Type III SS	
		d.f.	χ^2	P	χ^2	P
Treatment variables						
Landscape context	0.004	1	2.5	NS	0.4	NS
Fragment area ($\log_{10}$ + 1)	-0.359	1	73.7	**<0.001** ***	22.2	**<0.001** ***
Plant traits						
Life form		5	352.6	**<0.001** ***	105.5	**<0.001** ***
Fern	0.000					
Grass	-1.529					
Herbaceous dicot	-0.500					
Rush/sedge	-0.247					
Shrub/liane	-0.420					
Tree	-4.019					
Duration		2	299.9	**<0.001** ***	32.7	**<0.001** ***
Annual	0.000					
Biennial	0.342					
Perennial	0.952					
Dispersal mechanism – animal	-0.981	1	148.4	**<0.001** ***	26.8	**<0.001** ***
Dispersal mechanism – attachment	-0.678	1	216.3	**<0.001** ***	11.8	**<0.001** ***
Dispersal mechanism – ballistic	-0.116	1	210.4	**<0.001** ***	0.3	NS
Dispersal mechanism – water	0.588	1	0.9	NS	18.9	**<0.001** ***
Dispersal mechanism – wind	0.364	1	54.7	**<0.001** ***	4.9	**0.027** *
Dispersal mechanism – unspecialised	0.187	1	0.4	NS	1.0	NS
Shade tolerance		2	24.3	**0.018** *	54.4	**<0.001** ***
Low	-2.201					
Moderate	-1.882					
High	0.000					
Length of flowering period	-0.001	1	4.5	NS	0.0	NS
Introduction mode in NZ		2	610.4	**<0.001** ***	91.5	**<0.001** ***
Accidental	0.000					
Ornamental	-0.827					
Utility	1.332					
Year naturalised in NZ	-0.010	1	419.0	**<0.001** ***	17.2	**<0.001** ***
Number of regions occupied in NZ	0.152	1	381.4	**<0.001** ***	7.2	**0.007** **
Environmental weed status in NZ		1	185.8	**<0.001** ***	35.3	**<0.001** ***
No	0.000					
Yes	0.703					

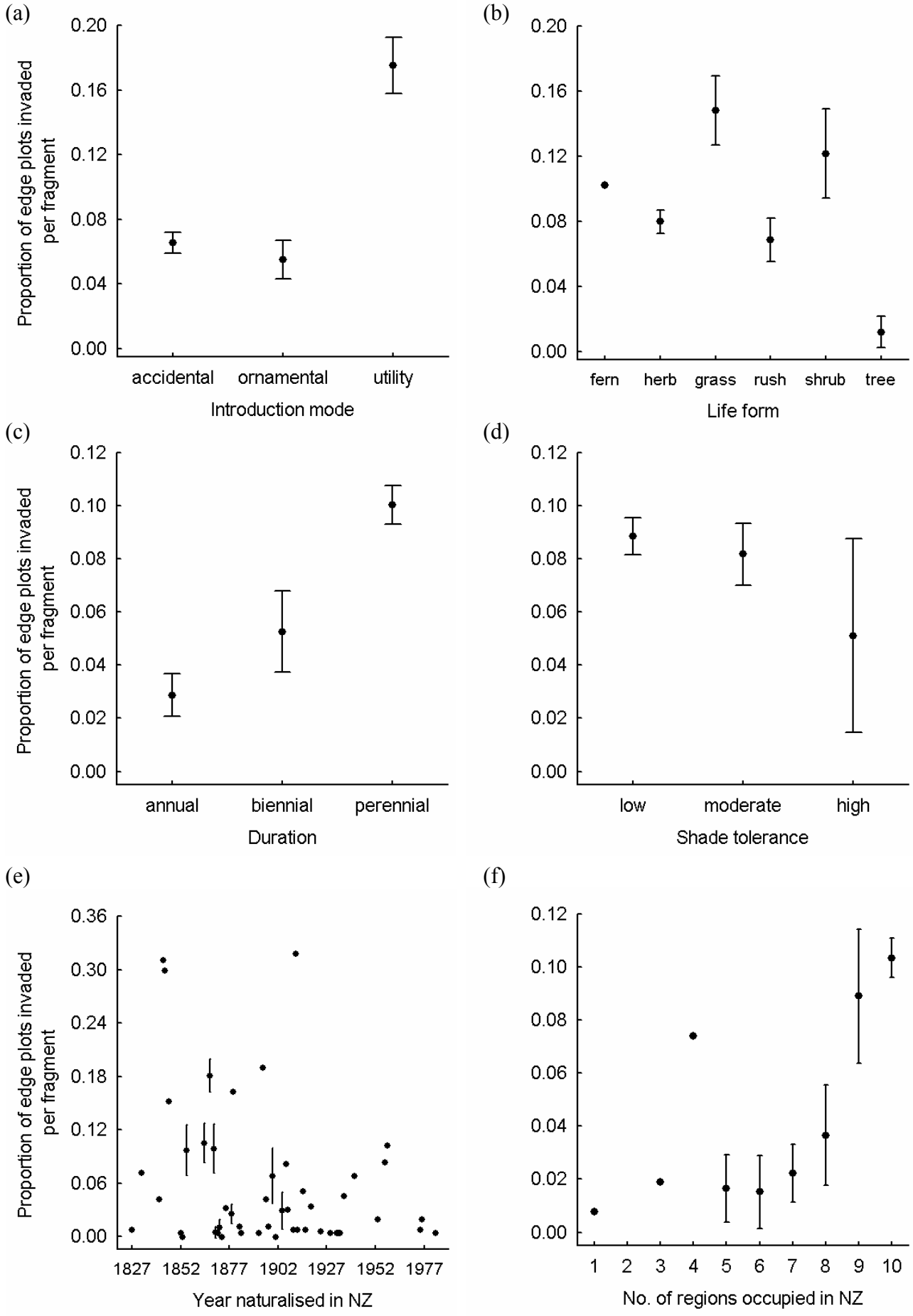


Figure 3.1 continued

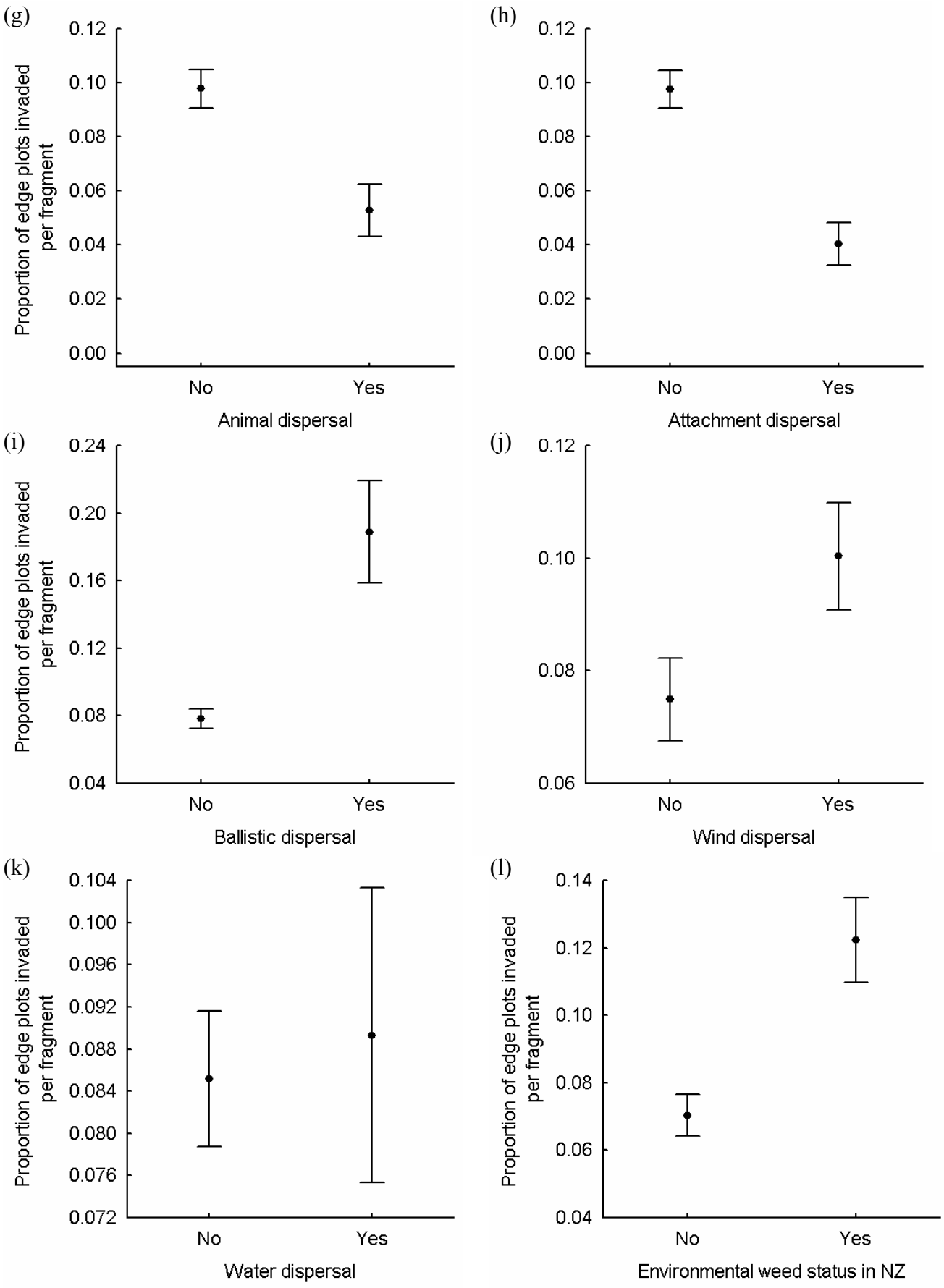


Figure 3.1. The effects of exotic plant traits on the mean proportion of edge plots invaded per fragment (edge distances from -8 to 2 m). See Methods for descriptions of the trait categories. Error bars are mean ±95% confidence intervals of values for species within each trait category.

The proportion of edge plots invaded per fragment decreased significantly with the year of naturalisation in New Zealand (**Table 3.2**), indicating that species introduced early to New Zealand tended to occupy more edge plots than recent naturalisations (**Figure 3.1e**). The number of regions occupied in New Zealand was highly correlated with the year of naturalisation ($n = 103$, $r = -0.623$, $p < 0.001$), meaning that exotic species that became naturalised early on are more widely distributed throughout New Zealand than recent naturalisations. The number of regions occupied in New Zealand had a highly significant Type I effect on the proportion of edge plots invaded per fragment, with species present in 9 or 10 regions of New Zealand invading the most edge plots (**Figure 3.1f**). The proportion of edge plots invaded per fragment was higher than expected for species occupying four regions in New Zealand, however these comprised just two exotic species (*Dryopteris dilatata* and *Juncus canadensis*) that were very common in the study area. The Type III effect (i.e. the additional effect when all the other variables were accounted for in the model) for the number of regions occupied ($\chi^2 = 7.2$, $p = 0.007$) was much weaker than the Type I effect ($\chi^2 = 381.4$, $p < 0.001$), presumably because most of the Type I effect was already explained by year of naturalisation. Environmental weed status was also an important predictor of invasiveness at fragment edges, as species listed as environmental weeds have invaded almost twice the proportion of plots per fragment as species not considered to be environmental weeds in New Zealand (**Figure 3.1l**).

3.3.3 The effects of plant traits on invasion into fragment interiors

The landscape treatment variable had no effect on the second response variable, however fragment area had a significant negative effect on the presence of exotic species in fragment interiors, indicating that larger fragments had fewer exotic plants present in interior plots (**Table 3.3**). Local propagule pressure in the matrix also had a significant influence on the response variable, as the presence of exotic species in fragment interiors increased in relation to their average percent cover in the matrix outside each fragment (**Table 3.3**).

After accounting for the treatment variables and local propagule pressure in the matrix, four of the plant traits had significant effects on the presence of exotic species in fragment interiors (**Table 3.3**). Shade tolerance was the most important predictor in the GLMs, with highly significant Type I and Type III effects (**Table 3.3**). As expected, species with a high degree of shade tolerance have invaded significantly more fragment interiors than species with low shade tolerance (*a priori* contrast, $p < 0.001$, **Figure 3.2a**). Life form had the second-largest influence on the response

variable (**Table 3.3**), with the fern *Dryopteris dilatata* having invaded more fragment interiors than the other life forms, and shrubs being the second-most invasive group (**Figure 3.2b**). In contrast, grasses, rushes and sedges have invaded the interiors of relatively few fragments. The effect of life form weakened when the fern category was removed from the analysis, and the Type III effect became marginally non-significant (Type III SS, $\chi^2 = 9.3$, $p = 0.050$), however the Type I effect remained significant (Type I SS, $\chi^2 = 16.9$, $p = 0.002$).

Duration (longevity) had a significant Type I effect on the presence of exotic species in fragment interiors, with perennials having invaded more interiors than biennials and annuals (**Figure 3.2c**). The Type III effect was non-significant, which indicates that most of the Type I effect was already explained by other influential traits such as shade tolerance and/or life form. Two dispersal mechanisms showed significant effects on exotic presence in fragment interiors – attachment (Type I SS, $\chi^2 = 13.6$, $p < 0.001$) and wind (Type III SS, $\chi^2 = 5.2$, $p = 0.023$). Species dispersed by attachment to animals have invaded the interiors of significantly fewer fragments than species without this dispersal mechanism (**Figure 3.2d**), whereas wind-dispersed species appeared to be more successful at invading fragment interiors than those lacking this mechanism (**Figure 3.2e**). The effect of introduction mode on the response variable was marginally non-significant (Type I SS, $\chi^2 = 5.7$, $p = 0.060$, **Table 3.3**), however plants introduced to New Zealand as ornamentals appear to have invaded more fragment interiors than plants introduced accidentally or for utility purposes (**Figure 3.2f**).

Table 3.3. The effects of species' traits on the presence of exotic plants in fragment interiors after accounting for the effects of landscape context and fragment area (edge distances from -128 to -16 m inside fragments). χ^2 values from Type I and Type III sums of squares from GLMs tested with binomial distributions are shown. Landscape context was defined by the percentage of native forest cover within a 3 km radius. Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*, NS = non-significant (p >0.05). See Methods for definitions of trait categories.

Predictors	Model estimate		GLM with Type I SS		GLM with Type III SS	
		d.f.	χ^2	P	χ^2	P
Treatment variables						
Landscape context	0.003	1	0.0	NS	0.0	NS
Fragment area ($\log_{10}$ + 1)	-0.601	1	8.5	**0.003** **	9.0	**0.003** **
Propagule pressure in matrix						
Mean percent cover in adjacent matrix	0.072	1	18.0	**<0.001** ***	18.1	**<0.001** ***
Plant traits						
Life form		5	36.5	**<0.001** ***	13.4	**0.020** *
Fern	0.000					
Grass	-2.367					
Herbaceous dicot	-1.109					
Rush/sedge	-2.724					
Shrub/liane	-0.354					
Tree	-1.159					
Duration		2	13.9	**<0.001** ***	3.4	NS
Annual	0.000					
Biennial	1.188					
Perennial	1.177					
Dispersal mechanism – animal	-0.562	1	0.2	NS	1.3	NS
Dispersal mechanism – attachment	-0.942	1	13.6	**<0.001** ***	2.4	NS
Dispersal mechanism – ballistic	0.534	1	0.0	NS	0.7	NS
Dispersal mechanism – water	0.056	1	2.3	NS	0.0	NS
Dispersal mechanism – wind	0.996	1	2.6	NS	5.2	**0.023** *
Dispersal mechanism – unspecialised	0.307	1	0.0	NS	0.4	NS
Shade tolerance		2	40.6	**<0.001** ***	28.9	**<0.001** ***
Low	-2.143					
Moderate	-0.563					
High	0.000					
Length of flowering period	0.002	1	1.9	NS	0.0	NS
Introduction mode in NZ		2	5.7	0.060 NS	1.0	NS
Accidental	0.000					
Ornamental	-0.371					
Utility	0.085					
Year naturalised in NZ	-0.003	1	0.5	NS	0.3	NS
Number of regions occupied in NZ	0.096	1	0.1	NS	0.5	NS
Environmental weed status in NZ		1	0.4	NS	0.3	NS
No	0.000					
Yes	-0.183					

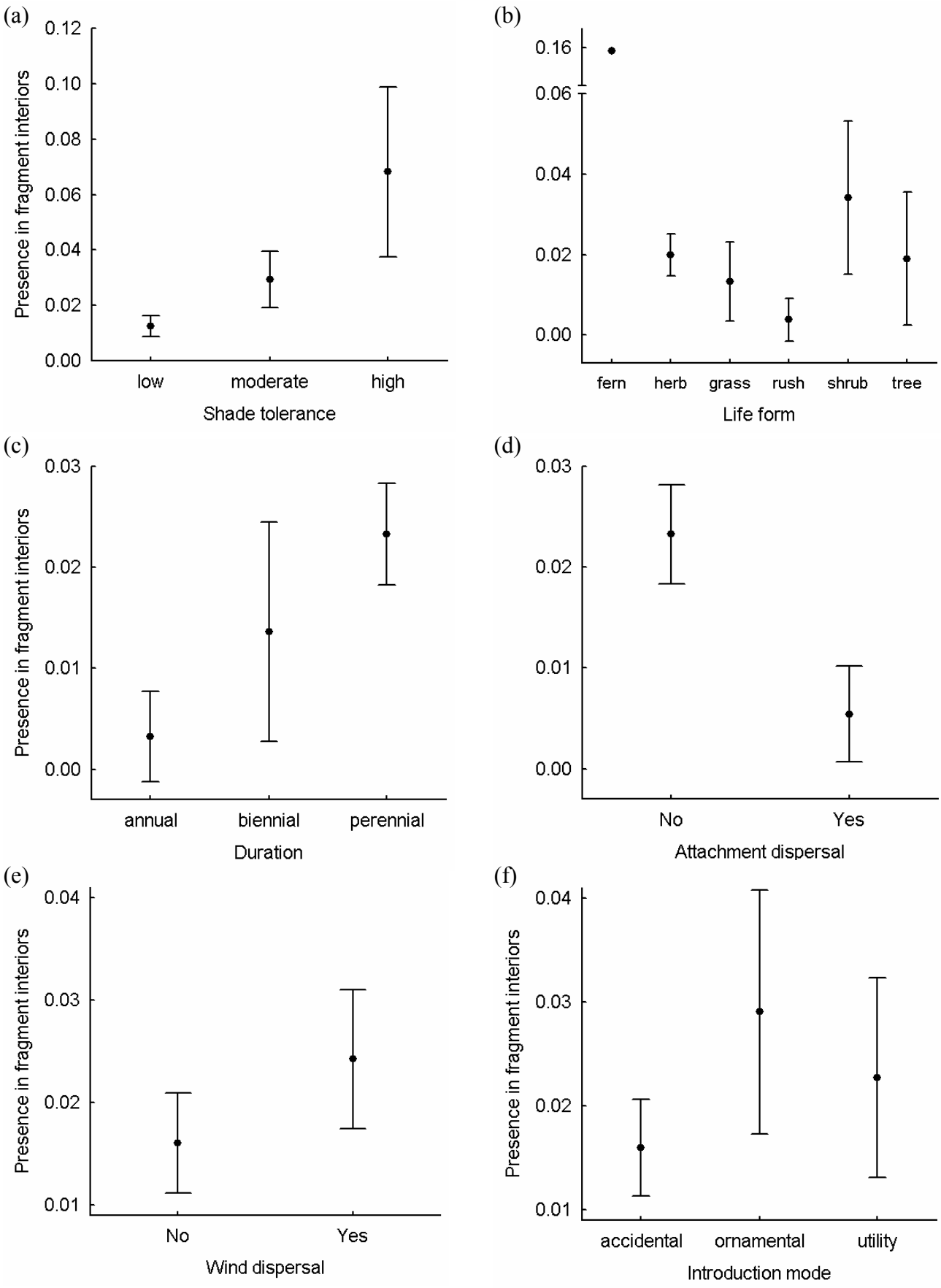


Figure 3.2. The effects of exotic plant traits on the mean presence of exotic plants in fragment interior habitats (edge distances from -128 to -16 m inside fragments). See Methods for descriptions of the trait categories. Error bars are mean ±95% confidence intervals of values for species within each trait category.

3.4 DISCUSSION

A combination of life history traits and the introduction mode, distribution and weed status of exotic plant species influenced their invasiveness in native forest fragments. Different traits were associated with invasiveness at the edges versus interiors of forest fragments, however, confirming that the importance of particular traits in contributing to invasion success is context-dependent (Alpert *et al.* 2000; Kolar & Lodge 2001; Richardson & Pysek 2006). A different set of species were successful at invading the edges of forest fragments than those invading interior habitats. Introduction mode was the most important predictor of plant invasiveness at forest edges, followed by year of naturalisation, whereas shade tolerance and life form were the most important predictors of invasion into forest interior habitats.

Species introduced to New Zealand for agricultural or horticultural purposes had invaded more plots at fragment edges than ornamental or accidental introductions. One explanation is that the landscapes of the study area are predominantly agricultural, and utility species have been widely planted by humans and are favoured by farm management regimes, hence their propagule pressure will be high (Pyšek *et al.* 2003). The conditions at fragment edges (i.e. disturbed, relatively high light and temperature levels) also appear to be suitable for species typically found in agricultural habitats. Despite the dominance of utility and accidental introductions in these landscapes, ornamental plants appeared to be more invasive in fragment interiors. The invasiveness of ornamental plants in natural areas has been recognised in a number of studies (Reichard & White 2001; Sullivan *et al.* 2005; Dehnen-Schmutz *et al.* 2007b; Milbau & Stout 2008), and is thought to be related to traits associated with plant selection and propagation such as fast growth, resistance to pests and diseases, and climatic suitability (Dehnen-Schmutz *et al.* 2007a; Lambdon *et al.* 2008). Invasions by ornamental plants are predicted to increase in New Zealand, as the number of naturalisations is increasing rapidly (Williams & Timmins 2002; Gatehouse 2008).

The majority of exotic species recorded in this study have been naturalised in New Zealand for more than 100 years. Similarly, a study by Williams and Wiser (2004) revealed that nearly 80% of exotic species in New Zealand braided riverbeds had been naturalised for more than 100 years. In my study, the year of naturalisation had a highly significant effect on the presence of exotic plants in forest fragments, with species that have been naturalised for more than 100 years being the most successful at invading native forest fragments. This is supported by the findings of other studies, which have found that introduction date is closely related to the probability of a species being established in the wild (Mulvaney 2001; Sullivan *et al.* 2004; Křivánek *et al.* 2006). For

example, a study on ornamental plants in Britain found that the longer a species had been present in Britain, the more likely it was to have established (Dehnen-Schmutz *et al.* 2007b). Other studies have also found a close relationship between early arrival and wide distribution (Scott & Panetta 1993; Williams & Wiser 2004; Castro *et al.* 2005; Hamilton *et al.* 2005; Wilson *et al.* 2007; Gatehouse 2008). The reason for this is probably because species that have been naturalised for a long time have had longer to disperse throughout the country and are likely to have a higher propagule pressure than more recent naturalisations (Castro *et al.* 2005). In my study, the number of regions occupied in New Zealand was highly correlated with the naturalisation year of each species, and consequently the number of regions occupied in New Zealand had a positive effect on the proportion of edge plots invaded per fragment. In addition, species that are widely distributed in their native range are expected to be able to spread widely outside their region of origin (Scott & Panetta 1993; Goodwin *et al.* 1999; Dehnen-Schmutz *et al.* 2007b; Gravuer *et al.* 2008; Milbau & Stout 2008; Ricklefs *et al.* 2008). This is because geographic range is likely to be correlated with other life history traits that allow a species to have a wide environmental tolerance, and therefore invade a range of habitats (Goodwin *et al.* 1999; Ricklefs *et al.* 2008).

Shade tolerance had a major influence on the invasiveness of exotic plants in my study, however the opposite characteristics were important in the two different habitats: low shade tolerance favoured invasion near forest edges, while high shade tolerance promoted invasion into shady, forest interior habitats. Several other studies have also highlighted the ability of shade-tolerant species to invade forest habitats (Gleadow & Ashton 1981; Hutchinson & Vankat 1997a; Martin & Marks 2006). Life form was also a significant predictor of plant invasiveness, at both the edges and interiors of forest fragments. Grasses, shrubs and ferns invaded more plots at edges than exotic trees, dicot herbs, rushes and sedges. The invasiveness of grasses at fragment edges is likely to be because most grasses are light-demanding, and have rapid growth rates and high seed production – characteristics which make them adept at colonising open, disturbed habitats (Grime 1979; Lake & Leishman 2004). In contrast, the fern *Dryopteris dilatata* appears to be highly invasive in the interiors of native forest fragments. *Dryopteris dilatata* is considered to be a forest interior specialist in its native range in Europe (Grashof-Bokdam 1997), and New Zealand native forests appear to offer similarly suitable habitat for this species. Fern characteristics which could contribute to their invasiveness in New Zealand forests are shade-tolerance, dispersal by wind and water, and being relatively unpalatable to stock. In spite of their potential to invade native forests, to my knowledge, no research has been carried out on the invasiveness of exotic ferns in New Zealand.

Exotic shrubs appeared to be relatively invasive in native forest fragments, both at edges and in interior habitats. The shrub group included three species of woody climbers/scramblers which are well-known for their invasiveness in New Zealand – *Hedera helix*, *Rubus fruticosus* and *R. laciniatus* (Craw 2000; Bellingham *et al.* 2004; Roy *et al.* 2004; Howell 2008). A number of studies have highlighted the invasiveness of lianes in natural areas (Daehler 1998; Williams & Timmins 1998, 2003; Lake & Leishman 2004), and an assessment by Howell (2008) confirmed that lianes had a high mean 'weediness score' and are over-represented among environmental weeds in New Zealand. Trees have been found to be invasive in forests elsewhere (Gleadow & Ashton 1981; Woods 1993; Daehler 1998; Gorchov & Trisel 2003; Mandryk & Wein 2006; Howell 2008), however there was little evidence for their invasiveness in this study, and very few exotic trees were recorded. One explanation is that propagule pressure from exotic trees is currently low in the study area. Relatively few exotic trees have been planted on the West Coast compared to other regions in New Zealand, because the predominant human land use on the West Coast is pastoral farming (with relatively little horticulture or forestry), and because the human population density and average income are relatively low (StatisticsNZ 2006), resulting in few ornamental plants in gardens. Another contributing factor is that many trees are slow to reproduce and can take a long time to increase their population sizes (Wangen & Webster 2006; Caley *et al.* 2008), therefore exotic woody species may not have had sufficient time to spread widely on the West Coast.

Longevity appeared to have an important influence on species' invasiveness, as perennials were much more successful at invading forest fragments than short-lived species. One explanation is that environmental conditions in native forests (i.e. relatively low levels of nutrients, light and disturbance) are likely to favour the survival and growth of long-lived species. Once established at forest fragments, perennials will be able to spread and exclude annuals and biennials, as the majority of these short-lived plants favour habitats with regular disturbances (Grime 1979).

Wind was the most common dispersal mechanism for exotic species recorded in this study and wind dispersal appeared to promote invasiveness in native forest fragments, as wind-dispersed species invaded more plots per fragment and more fragment interiors than species lacking this dispersal mechanism. Wind dispersal appears to convey an advantage in deforested landscapes, where wind speeds may be high due to a lack of resistance from tall vegetation (Laurance & Curran 2008). In addition, wind dispersal is usually associated with small seed size, which has been linked with invasiveness in plants (Rejmanek 1996; Rejmánek & Richardson 1996; Kolar & Lodge 2001; Hamilton *et al.* 2005). In contrast, species dispersed by animals appeared to be less

invasive in forest fragments. A possible explanation for this is that the spread of exotic animal-dispersed limited in the study area because populations of their animal mutualists, which are predominantly exotic species (Williams & Karl 1996), may be are relatively low on the West Coast because of a lack of suitable habitat.

Species classified as environmental weeds in New Zealand have invaded more plots at fragment edges than non-weedy species. This is to be expected, perhaps since the success of an invader in one location is known to be a good predictor of invasiveness in other areas (Scott & Panetta 1993; Reichard & Hamilton 1997). Surprisingly, however, environmental weed status had no effect on invasion success in fragment interior habitats. One explanation for this is that many plant species that are relatively common in forest fragments on the West Coast are not classified as environmental weeds because they are not considered to threaten native communities (e.g. *Mycelis muralis, Digitalis purpurea, Prunella vulgaris*) (Howell 2008).

In conclusion, traits associated with plant invasiveness near the edges of forest fragments were: being a perennial, a monocot, shrub or fern, having low shade tolerance, wind dispersal, being introduced early to New Zealand, for agricultural or horticultural purposes, and having a wide geographic range in New Zealand. In contrast, traits promoting invasiveness in forest interior habitats were: being a perennial, a fern or shrub, having high shade tolerance, wind dispersal, and being introduced for ornamental reasons. Other traits likely to influence invasiveness of exotic plants include growth rate, reproductive output, and dispersal power, however these data are often lacking or unreliable (Richardson & Pysek 2006), hence they were not included in this study. It should be acknowledged that most naturalised plant species are still expanding their populations in New Zealand, hence their distribution and abundance have not reached equilibrium (Williams & Wiser 2004). This makes it difficult to determine the potential range of habitats able to be invaded by each species, and to define which traits promote invasiveness in different environments, as species' traits may be weakly related to environmental conditions (Wiser *et al.* 1998). In conclusion, further research is needed on the importance of plant traits and their interactions with human activities in influencing propagule pressure and the different stages of the invasion process, under varying environmental conditions. This information will be crucial for refining methods of predicting which species are likely to become invasive in different situations, and enabling us to better prevent and manage invasions.

Chapter 4 – Interactions between landscape cover and edge effects on exotic plant invasions: an experimental test in native forest fragments

4.1 INTRODUCTION

A number of recent studies have suggested that landscape context is likely to have an important influence on invasions in fragmented landscapes (With 2002; Charbonneau & Fahrig 2004; Pauchard & Alaback 2004; Deckers *et al.* 2005; Bartuszevige *et al.* 2006; Henderson *et al.* 2006; Duguay *et al.* 2007; Nesslage *et al.* 2007). Landscapes which have lost a high proportion of native forest cover are expected to be more heavily invaded by exotic plants because conditions in these landscapes favour the establishment and spread of exotic plants (leading to higher exotic propagule pressure), and fragments in these landscapes are likely to be more susceptible to invasion by exotic plants (i.e. have higher invasibility) (With 2002; With 2004; Kupfer *et al.* 2006). There are a number of potential mechanisms that could drive these trends. Firstly, the propagule pressure of exotic plants is expected to be higher in more heavily deforested landscapes because the intensity of human land use is higher (Geist & Lambin 2002; Fischer & Lindenmayer 2007), and the abundance of exotic plants is usually closely correlated with these factors (Lonsdale 1999; Cadotte & Lovett-Doust 2001; Charbonneau & Fahrig 2004; Sullivan *et al.* 2004; Sullivan *et al.* 2005).

Secondly, fragments in heavily deforested landscapes are likely to experience higher levels of disturbance (McIntyre & Hobbs 1999; With 2002; Fischer & Lindenmayer 2007), and disturbance appears to increase fragment invasibility, as it is often cited as a key factor driving plant invasions in forest fragments (Amor & Piggin 1977; Hobbs & Atkins 1988; Hobbs 1989; Bellingham *et al.* 2005; Guirado *et al.* 2006; Wiser & Allen 2006). Types of disturbance in forest fragments include grazing by domestic and wild animals (Yates *et al.* 2000; Hobbs 2001), logging (Echeverría *et al.* 2007), fires (Cochrane 2001), nutrification (Duncan *et al.* 2008), and drainage (Sousa 1984; Hobbs & Huenneke 1992). Deforestation also leads to increased wind speeds in fragmented landscapes, which cause increased damage to trees and wind-throw, thus increasing light levels which may promote invasion (Hobbs 1993; Laurance & Curran 2008). Increased soil fertility is likely to favour the establishment of exotic plant species, as they often have a greater capacity than native species to utilise elevated nutrient levels (Amor & Piggin 1977; Allcock 2002; King & Buckney 2002; Craine *et al.* 2006). For example, an experimental study revealed that invasive exotic plants had higher survival rates and a larger biomass increase with nutrient addition than

native species, and suggested that nutrient-enrichment may have facilitated invasion of exotic species in low-fertility sandstone areas in Australia (Leishman & Thomson 2005). Similarly, another study found that increased soil nutrients were associated with exotic plant invasions in urban bushland in Sydney (King & Buckney 2002).

Fragment edges are often focal sites for plant invasions, as edges are usually the first point of contact for fluxes of organisms, material and energy from the surrounding landscape into forest fragments (Cadenasso & Pickett 2001; Weathers *et al.* 2001). Forest edges typically experience higher light, temperature and nutrient levels than forest interiors (Saunders *et al.* 1991; Davies-Colley *et al.* 2000; Weathers *et al.* 2001), and this is likely to promote the establishment and growth of exotic plants (Brothers & Spingarn 1992). A number of previous studies (Donovan *et al.* 1997; Hartley & Hunter 1998; Driscoll & Donovan 2004) and my own observational data from West Coast forest fragments (see **Chapter 2** of this thesis) have highlighted the important consequences of interactions between landscape cover and edge effects in fragmented landscapes. In **Chapter 2**, I found a significant interaction between landscape forest cover and edge effects on plant community composition (evident by a change in the strength of the edge gradient in species composition in relation to forest cover in the landscape), indicating that edge effects were more severe in fragments in heavily deforested landscapes. (The potential reasons for this are discussed in **Chapter 2**, therefore I will not repeat them here). Although interactions between landscape cover and edge effects could have important implications for managing the spread of invasive species in fragmented landscapes, there has been very little research on these interactions or their role in invasion processes (With 2002).

The aim of this research was to investigate the effects of landscape cover and edge effects on exotic plant invasion success in fragments and to test for interactions between these effects, using native forest fragments on the West Coast as the study system. Because of the complexity of factors affecting different stages of the plant invasion process, and difficulty in measuring propagule pressure, an experimental approach was needed to tease apart the different mechanisms underlying the invasion process (Lavorel *et al.* 1999; Richardson & Pysek 2006). Experimental addition of exotic plant propagules was used to investigate the invasion success of exotic plant species in relation to edge gradients within landscapes with varying amounts of native forest cover. This would allow me to explore whether propagule availability (i.e. propagule pressure) and/or habitat suitability (invasibility) may be limiting invasions of exotic plants in forest fragments (Moore & Elmendorf 2006). Because species traits are likely to have a major influence on their responses to landscape cover and edge effects (see **Chapter 3**), I carried out the

experiments using five species from two different functional groups. Landscape cover and edge effects may interact with different stages of the plant invasion process in different, potentially contrasting ways (With 2002; Dietz & Edwards 2006), therefore experiments were carried out to determine germination, seedling survival and growth rates of exotic plants in forest fragments, in order to understand the different mechanisms limiting success at each stage.

4.2 METHODS

4.2.1 Study area

The study was carried out in the Grey and Buller Districts on the West Coast of the South Island of New Zealand (42°08' to 42°36' and 171°25' to 171°46'). See **Chapter 2, section 2.2.1** for a full description of the study area.

4.2.2 Landscape and fragment selection

The study was conducted in native forest fragments in five landscapes with varying percentages of native forest cover, ranging from 16% to 60% (see **Figure 4.1**). The percentage of forest cover in each landscape was calculated within a circle with a 3 km radius centred on each forest fragment. See **Chapter 2, section 2.2.2** for a full description of the methods used to select landscapes and fragments. It was not logistically feasible to experimentally examine the effects of fragment area in addition to landscape cover and edge effects, therefore one native forest fragment of a standard size (in the 2-8 ha size category) was selected as a study site in each landscape:

6.5 ha fragment in a landscape with 16.0% forest cover (Weka6)
2.4 ha fragment in a landscape with 23.8% forest cover (BerryP)
6.2 ha fragment in a landscape with 40.0% forest cover (Thompson6)
5.8 ha fragment in a landscape with 46.8% forest cover (Bell Hill5)
4.6 ha fragment in a landscape with 57.5% forest cover (Ferguson71)

4.2.3 Selection of edge gradients

See **Chapter 2, section 2.2.3** for a full description of the methods used to select the edge gradient sampled at each forest fragment. Because it was not logically feasible to carry out the propagule addition experiments at all edge distances, a subset of only five edge distances was used: -0.33, -4, -8, -16, and -32 m from the edge (forest plots were coded as negative).

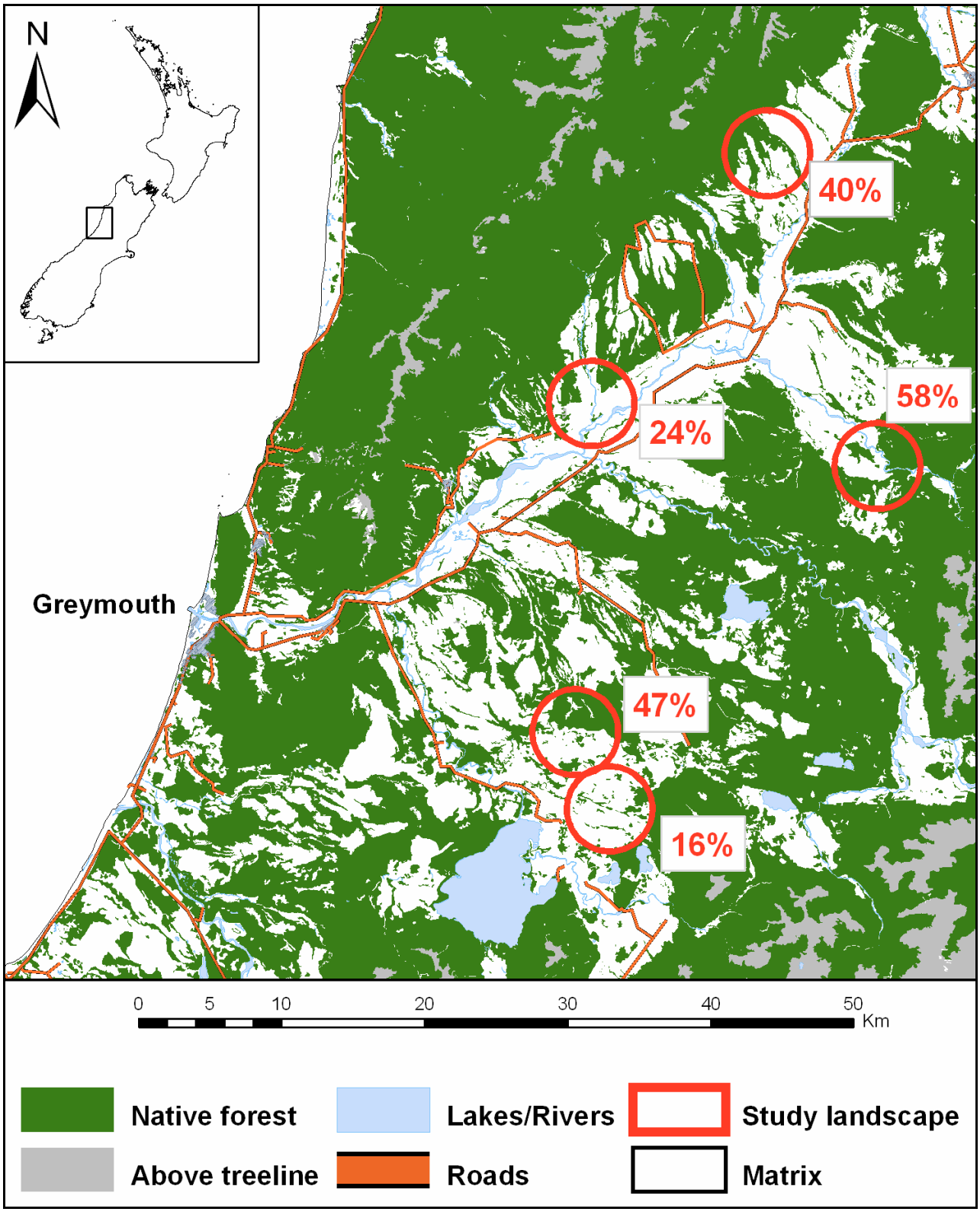


Figure 4.1. Location of the five study landscapes (3-km radius circles) in the Grey and Buller Districts, West Coast, New Zealand (42°10' to 42°35' and 171°33' to 171°41'). Landscapes contained 16%, 24%, 40%, 47%, and 58% native forest cover. Land cover was determined from the NZ Land Cover Database version 2 (MfE 2004).

4.2.4 Exotic plant species used in the propagule addition experiments

Propagule addition experiments were conducted using five exotic plant species: *Hedera helix* L. (ivy, Araliaceae), *Prunella vulgaris* L. (selfheal, Lamiaceae), *Crataegus monogyna* Jacq. (hawthorn, Rosaceae), *Sorbus aucuparia* L. (rowan, Rosaceae) and *Digitalis purpurea* L. (foxglove, Scrophulariaceae). The species were chosen because they had all been recorded in native forest fragments in the study area (see **Appendix 3**), and represented two contrasting functional groups: (1) herbaceous, short-lived species with unspecialised dispersal (*D. purpurea* and *P. vulgaris*), and (2) woody, bird-dispersed perennials (*C. monogyna*, *S. aucuparia* and *H. helix*).

Digitalis purpurea is a widespread biennial or short-lived perennial herb, originally from south-west and central Europe (Webb *et al.* 1988). *Digitalis purpurea* is common in poor pastures, second-growth forest, disturbed ground, and waste places, and is particularly abundant in the wetter parts of New Zealand (Webb *et al.* 1988; Roy *et al.* 2004). *Prunella vulgaris* is a creeping, mat-forming perennial up to 30 cm tall, originally from the temperate northern hemisphere (Roy *et al.* 2004). *Prunella vulgaris* is common throughout New Zealand, being found in damp lawns and lime-deficient pastures, forest margins and clearings (Roy *et al.* 2004). *Crataegus monogyna* is a thorny shrub or small tree up to 10 m tall, widely planted in hedgerows, and originally from Europe. *Crataegus monogyna* produces clusters of shiny red fruit, dispersed by birds (Williams & Buxton 1986), and is found in a wide range of habitats in urban and rural areas such as roadsides, scrub-covered and grassy hillsides, disturbed forest and waste places (Webb *et al.* 1988). *Sorbus aucuparia* is a deciduous tree up to 12 m tall from Eurasia, which produces clusters of bird-dispersed fruit (Webb *et al.* 1988). *Sorbus aucuparia* occupies roadsides, plantation margins, stony scrub and wasteland in coastal and inland areas up to 900 m a.s.l. (Webb *et al.* 1988). *Hedera helix* is a perennial woody climber, originally from temperate Europe and Asia (Roy *et al.* 2004). *Hedera helix* is widely cultivated ornamentally in New Zealand and produces black fruits which are readily eaten and dispersed by birds, allowing it to invade a range of habitats such as disturbed forests, waste places, river beds, stream banks, and cliffs (Webb *et al.* 1988; Roy *et al.* 2004). *Crataegus monogyna*, *H. helix* and *S. aucuparia* are listed as environmental weeds in a recent assessment by the Department of Conservation (Howell 2008).

Fruit and seeds were collected from wild plants of *D. purpurea*, *P. vulgaris*, *C. monogyna* and *S. aucuparia* in the study area during May 2005. *Hedera helix* fruit was collected from roadsides in Christchurch during October 2005. *Sorbus aucuparia*, *C. monogyna* and *H. helix* seeds were

manually removed from fruit and cleaned in cold water; *Digitalis purpurea* and *P. vulgaris* seeds were extracted from inflorescences. Seeds were stored in a refrigerator at 4°C for up to four months until ready for sowing.

4.2.5 Seed germination in forest fragments

Seeds of the five study species were sown in the 15 x 2 m survey plots at three distances from the forest edge: -0.33, -8 and -32 m inside fragments (only three distances were used because of logistical limitations such as the number of trays and seeds available). Seeds were sown in free-draining 300 x 200 x 60 mm deep plastic trays filled with sterilised potting mix with a slow-release plant fertilizer. Potting mix was used in order to standardise soil characteristics in all of the trays, and to enable me to compare germination and seedling growth responses. Five trays were placed in each plot, with all five species in each tray. The trays were sunk level into the ground in order to increase contact with the soil and reduce fluctuations in temperature and moisture. The number of seeds placed in each tray varied between species (**Table 4.1**). *Prunella vulgaris* and *D. purpurea* seeds were placed in opposite corners of the trays in order to minimise inter-specific competition between emerging seedlings, as these species were expected to grow the fastest, and occupy the most space. The position of the other species in the tray was randomised. Trays were covered with a thin layer of fern fronds in order to shade them and discourage interference by birds. Trays were placed out in fragments in May 2006 and germination was recorded in January 2007.

Table 4.1. Number of exotic plant propagules added at each distance from the forest edge in each of the five study landscapes. [a] only 10 *Hedera helix* seeds were sown at each position at the Weka6 site (16% forest cover in the landscape), [b] only 10 *Prunella vulgaris* seedlings were planted at 32 m at the Ferguson71 site (58% forest cover in the landscape).

	Distance from the forest edge (metres)					Total in five landscapes
	-0.33	-4	-8	-16	-32	
SEEDS						
Crataegus monogyna	80	-	80	-	80	1200
Digitalis purpurea	375	-	375	-	375	5625
Hedera helix	20[a]	-	20[a]	-	20[a]	270
Prunella vulgaris	80	-	80	-	80	1200
Sorbus aucuparia	80	-	80	-	80	1200
SEEDLINGS						
Digitalis purpurea	5	-	5	-	5	75
Hedera helix	12	10	12	10	12	280
Prunella vulgaris	14	12	14	12	14[b]	326

4.2.6 Seed germination under laboratory conditions

Seeds of all species were sown under laboratory conditions to provide an indication of germination rates under controlled conditions and to produce seedlings for use in the field experiments. At least 1000 seeds of each species were sown in plastic multi-cell trays filled with sterilised seed raising mix with 1.2 g/L Superphosphate fertilizer (containing 9.3% phosphorus, 10.8% sulphur and 20.0% calcium) and 0.6 g/l dolomite lime. Trays were placed in controlled temperate growth cabinets for approximately two months from October to December 2005. All species were placed under the same conditions: a constant temperature of 22°C, with 16 hours of light per day. Trays were watered every 1–3 days and germination recorded. After two months, all of the multi-cell trays were transferred to an unheated glasshouse (where air temperature ranged from 12 to 28°C), in order to harden off seedlings before use in the field experiment. Trays were watered as required and further germination recorded. Seedlings emerging in the multi-cell trays were transferred to plastic pots (measuring 120 x 180 x 70 mm) filled with sterilised potting mix containing a slow-release plant fertilizer when they reached approximately 10 mm high.

4.2.7 Seedling growth in forest fragments

Hedera helix and *P. vulgaris* seedlings were planted in the 15 x 2 m survey plots at five distances from the edge (-0.33, -4, -8, -16, and -32 m), and *D. purpurea* seedlings were planted at three distances (-0.33, -8 and -32 m). The number of seedlings planted varied among the three species, depending on the availability of seedlings produced in the laboratory germination trials (see **Table 4.1**). *Crataegus monogyna* and *S. aucuparia* were not able to be used in the seedling growth experiments because no seeds germinated in the lab. Seedlings were planted out in plastic pots (120 x 180 x 70 mm deep) in order to minimize damage to roots and enable them to be easily located and removed at the end of the experiment. Slits were cut into the sides of each pot to reduce potential root crowding and increase contact with the soil. Seedlings of each species were spread out as much as possible within each plot and were at least 15 cm apart. Plots were fenced with one metre high 50 mm hexagonal wire mesh in order to avoid interference by weka (*Gallirallus australis* subsp. *australis*), an inquisitive flightless native bird. Seedlings were planted in the fragments in May 2006 and harvested in January 2007. The height and number of leaves of seedlings were recorded at the beginning and end of the experiment. Seedling height was measured by pulling the longest stem straight. Some *P. vulgaris* and *D. purpurea* seedlings produced flowers, therefore the number of flowers per seedling was recorded.

4.2.8 Environmental variables

Treatment variables

The three treatment variables comprised forest cover in the landscape, distance from the forest edge, and a landscape by distance from edge interaction term. Landscape was defined by the percentage native forest cover in each landscape (circle with a 3 km radius), and ranged from 16.0% to 57.5%. Distance from the forest edge was $\log_2$ transformed and coded as negative for distances inside the forest (Ewers & Didham 2006b).

Environmental covariates

In addition to the treatment variables, a number of environmental covariates were measured, as these were also likely to influence plant responses and could potentially confound or explain the treatment effects (**Table 4.2**). The covariates comprised three groups of factors: microclimate, soil, and vegetation. Hobo™ dataloggers (Onset Computer Corporation) were used to record air temperature (°C) and relative humidity (%) in each plot. Dataloggers were mounted on stakes and held 60 cm above the ground in the centre of each plot, and readings were taken every 15 minutes for a minimum of 10 days during February and March 2006. Hemispherical photographs of the canopy were taken in each plot in order to provide an indirect estimate of light intensity. A Nikon Coolpix 5700 digital camera with a FC-E9 fisheye lens (183° angle of view) was mounted approximately 1 m off the ground with a tripod and aligned to magnetic north. Photographs were taken during cloudy conditions to minimize the effect of sun flecks and variability in the amount of sunlight between plots. The aperture was set at F/7.1 and shutter speed to 1/15 second in order to standardise the exposure. Percentage canopy cover was calculated from the hemispherical photographs using Gap Light Analyser version 2 software (Frazer *et al.* 1999).

Soil samples were taken in each plot using a soil auger driven to a depth of 20 cm. A minimum of six cores were taken from each plot and bulked. Samples were air dried, then ground through a 2 mm sieve. Total carbon, phosphorus, nitrogen, organic matter content and pH were determined by Analytical Research Laboratories Ltd, Napier, New Zealand. Available soil phosphorus was measured using Olsen's method (Olsen *et al.* 1954). Total nitrogen was analysed with a LECO analyser using the Dumas method (Petit *et al.* 2004), where soils are introduced into a combustion furnace and oxidised in a stream of pure oxygen. The subsequent gas stream was analysed for nitrogen dioxide by a thermal conductivity detection cell and the results expressed as total nitrogen.

Total carbon was analysed by the combustion method using a LECO Analyser, and organic matter content was calculated from organic carbon using a standard mathematical conversion (Peverill *et al.* 1999). The carbon to nitrogen ratio (C/N ratio) was also calculated, as this provides a good indication of the availability of nitrogen in the soil (lower C/N means higher nitrogen availability).

Vegetation at the study sites was surveyed from January to March 2005 and November 2005 to February 2006. The percent foliage cover of native and exotic vascular plant species in each plot was estimated in two height tiers: ground (<0.5 m) and shrub (0.5 – 2 m). Species not able to be identified in the field were collected, and specimens were later identified using taxonomic keys (Allan 1961; Healy & Edgar 1980; Webb *et al.* 1988; Edgar *et al.* 2000) or sent to Landcare Research Plant Identification Service (Lincoln, Canterbury, New Zealand).

Table 4.2. Environmental variables used as predictors in generalised linear models (GLMs) of plant germination, growth and flowering responses at forest fragments in five different landscapes. LCDB2 = New Zealand Land Cover Database version 2 (MfE 2004).

Variable	Description	Units	Data source
Treatments			
Landscape	Percentage native forest cover in landscape (within a 3-km radius)	%	LCDB2
Edgedist	Log_2 distance from forest edge	m	
Landscape x Edgedist	Landscape by Edgedist interaction		
Covariates			
Microclimate	Axis 1 scores from a PCA of mean daytime temperature, mean daytime relative humidity and percent canopy cover		Dataloggers, Canopy photos
pH	Soil pH	0-14	Soil samples
N	Soil total nitrogen	% w/w	Soil samples
P	Soil phosphorus	ug/mL	Soil samples
C/N	Soil carbon/nitrogen ratio		Soil samples
Vegetation	Axis 1 sample scores from a DCA of plant species composition (<2 m in height)		Field survey

4.2.9 Statistical analyses

Germination success (proportion germinated), mean number of days until germination, and mortality rate (%) were calculated for each species in the laboratory germination trials. In the field germination experiments, the mean proportion of seeds that germinated in each plot (five trays per plot) was calculated, in order to measure germination success at each edge distance. In the seedling growth experiments, overall mortality for each species was recorded, and the height growth relative to the initial height was calculated for each seedling.

Generalised linear models (GLMs) were used to analyse the relationships between plant germination, growth and flowering responses and the environmental variables (see **Table 4.2**). GLMs were used because they are relatively robust when data are not normally distributed and can include both factorial and continuous predictor variables (Quinn & Keough 2002). R version 2.4.1 software (RFoundation 2006) was used to carry out all of the GLMs. Data for relative height growth and the number of flowers per seedling were log-transformed ($\log_{10} + 0.1$) to produce normal distributions. GLMs for the germination data used logit link functions and quasibinomial distributions, as the germination data were proportions and over-dispersion was detected in the data. GLMs for relative height growth and the number of flowers per seedling used identity link functions and gaussian (normal) distributions. Separate models were run for each species.

Models with treatment variables only

In order to determine the effects of the treatment variables on plant responses, the GLMs had to take into account the hierarchical nature of the sampling design i.e. edge distances were arrayed within the single fragment sampled in each landscape. Because of this spatial hierarchy, Type I (sequential) sums of squares (SS) were used to determine the significance of the treatment effects, adopting a regression approach of Sokal and Rohlf (1995, p. 476) that accounts for non-independence among multiple values of Y for each value of X. Taking a sequential approach, I was initially interested in whether the response variables differed significantly between the five sites (Weka6, BerryP, Thompson6, BellHill5 and Ferguson71), and whether these differences aligned significantly as a continuous function of the percentage of native forest cover in the landscape surrounding the sites. Next, within fragments, I was interested in whether the response variables differed significantly between the five sampling plots (-0.33, -4, -8, -16, and -32 m), and whether these differences aligned significantly as a continuous function of distance from the forest edge. Most importantly, I was interested in whether there was a significant interaction between the effects of forest cover in the landscape and distance from the forest edge on the response variables i.e. whether the relationship between distance from the forest edge and the response variables varied in relation to the percentage of forest cover in the landscape.

To test these effects, a composite ANOVA table had to be created in a sequential manner (see **Table 4.3** for an example). First, a GLM with Type I SS was created with Site, Plot and the interaction between Site and Plot all entered as categorical variables, testing stochastic variation in the response variables from site to site, and from plot to plot. The significance of the Site and Plot factors was tested with corrected F-values calculated using the mean squares (MS) of the Site x

Plot interaction as the denominator error term, as this used the correct denominator degrees of freedom (df). The F-value for the Site x Plot interaction was calculated using the Total Error as the denominator error term. Second, a GLM with Landscape (percentage forest cover in the landscape) as a continuous variable was used to test whether there was a significant linear regression between the percentage of forest cover in the landscape and the response variables. The significance of the Landscape regression was determined with an F-value calculated using the MS of the deviation from the Landscape regression as the denominator error term. The SS and df for the deviation from the Landscape regression were calculated by subtracting the Landscape SS from the Site SS, and the Landscape df from the Site df (see **Table 4.3**). Third, a GLM with Type I SS was created with Site and Edgedist (distance from the forest edge), with Edgedist being entered as a continuous variable. The significance of the Edgedist regression was determined in a similar way to the Landscape regression i.e. with an F-value calculated using the MS of the deviation from the Edgedist regression as the denominator error term. Similarly, the SS and df for the deviation from the Edgedist regression were calculated by subtracting the Edgedist SS from the Plot SS, and the Edgedist df from the Plot df. Finally, a GLM was created with Site, Plot, and the Landscape x Edgedist interaction variable entered as a continuous variable. The significance of the Landscape x Edgedist regression was determined with an F-value calculated using the MS of the deviation from the Landscape x Edgedist regression as the denominator error term. Again, the SS and df for the deviation from the Landscape x Edgedist regression were calculated by subtracting the Landscape x Edgedist SS from the Site x Plot SS, and the Landscape x Edgedist df from the Site x Plot df. An R^2 value was calculated for each regression by dividing the regression SS by the Total SS.

Table 4.3. Effects of the treatment variables on percentage germination of *Digitalis purpurea* seeds in fragments in five landscapes. Treatment variables: **Landscape** = percentage of native forest cover in the landscape, **Edgedist** = $\log_2$ distance from the forest edge (m), **Landscape x Edgedist** = Landscape x Edgedist interaction. This composite ANOVA table was created from the results of four separate GLMs (see Methods for details). Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*.

Digitalis purpurea	**SS**	**d.f.**	**MS**	**F**	**P**
Site factor	0.137	4	0.034	0.604	0.671
Landscape regression	0.011	1	0.011	0.257	0.647
deviation from Landscape regression	0.126	3	0.042		
Plot factor	0.232	2	0.116	2.049	0.191
Edgedist regression	0.220	1	0.220	17.910	0.148
deviation from Edgedist regression	0.012	1	0.012		
Site x Plot interaction	0.453	8	0.057	6.074	**<0.001*** **
Landscape x Edgedist regression	0.063	1	0.063	1.140	0.321
deviation from Landscape x Edgedist regr.	0.390	7	0.056		
Error	0.559	60	0.009		
Total	1.381	74			

Models with environmental covariates

A Pearson correlation matrix was constructed between all 10 of the measured environmental covariates to determine whether any of them could be omitted from the GLMs. Soil nitrogen was highly correlated with soil carbon ($n = 25$, $r = 0.97$, $p < 0.001$) and organic matter content ($n = 25$, $r = 0.97$, $p < 0.001$), therefore only soil nitrogen was included as a predictor in the GLMs. Soil nutrients (nitrogen, phosphorus, and C/N ratio) were not included as covariates in the seed germination experiments, because seeds were sown in trays with potting mix and should have been relatively unaffected by soil nutrients at each site. Principle components analysis (PCA), a linear ordination technique, was used to reduce the three microclimatic variables (percent canopy cover, air temperature and relative humidity) into one composite variable. The first axis of the PCA explained a substantial amount of the variation in the data (70% of the total variance), so this was used as a predictor in the GLMs (called 'microclimate') instead of the individual variables.

Detrended correspondence analysis (DCA), a multivariate ordination technique, was used to characterise vegetation composition in the survey plots. DCA was used instead of linear ordination methods such as PCA because the gradient lengths were relatively long (i.e. >4) (Hill & Gauch 1980; Lepš & Šmilauer 2003). Percent cover data were converted to cover scores using the formula (David Norton, pers. comm.):

$$\text{Cover score} = \sum \% \text{ cover} \times \log_{10}(\text{tier depth})$$

and these comprised the species data in the DCA. Downweighting of 'rare' species and detrending by segments were selected using CANOCO 4.02 software (1997-1999 GLW-CPRO, Centre for Biometry, Wageningen, The Netherlands).

In the GLMs, covariates were entered as predictors ahead of the treatment variables, in order to partial out their potentially confounding effects on the response variables and to assess whether the covariates changed the effects of the treatment variables. Composite ANOVA tables were constructed again using the method described above for the Treatment-only model. The influence of each covariate was determined by comparing the R^2 values for the Landscape, Edgedist and Landscape x Edgedist regressions from the Treatment-only model with the R^2 values from a model with that covariate added ahead of the treatment variables. If the Landscape x Edgedist regression was not significant in the Treatment-only model, and did not become significant when any of the covariates were initially added, then no further models were run. However, if the Landscape x Edgedist regression was significant with any of the covariates in the model, then the

covariate which resulted in the biggest increase in the R^2 for the Landscape x Edgedist regression (i.e. had the biggest confounding effect) was retained in the model, and separate GLMs were run with each of the remaining covariates added first in the model. Again, the covariate which produced the biggest increase in the R^2 for the Landscape x Edgedist regression (in comparison to the model with one covariate) was retained in the model. The process above was repeated until all of the covariates had been added to the Treatment-only model. In some models, the addition of a covariate improved the R^2 value, but the P-value actually became less significant because each time a covariate was added, the denominator degrees of freedom decreased by one, making it more difficult to achieve a statistically significant P-value. If the addition of covariates reduced the R^2 for the Landscape x Edgedist regression, then the covariate which produced the biggest reduction was retained in the model, and the process was repeated until all of the covariates had been added to the model. This approach enabled me to determine whether the covariates explained some of the treatment effects on the response variables.

4.3 RESULTS

4.3.1 Seed germination under laboratory conditions

Species showed differences in seed germination and mortality rates after six months under controlled conditions in the laboratory and glasshouse. *Hedera helix* had the highest germination success (40.1% of seeds sown germinated), followed by *P. vulgaris* (39.5%), and *D. purpurea* (10.4%). None of the *C. monogyna* or *S. aucuparia* seeds germinated after seven months in the lab. *Hedera helix* had the fastest mean germination time, with seeds taking 14 days on average to germinate (**Table 4.4**). *Digitalis purpurea* seeds took four times longer than *H. helix* to germinate (66 days on average), and *P. vulgaris* seeds took even longer (87 days on average). *Hedera helix* had the highest mortality rate, with more than 14% of seedlings dying after germination.

Table 4.4. Seed germination and mortality rates of five exotic plant species after six months under laboratory conditions.

Species	Number of seeds sown	Number of germinated seeds (% of sown)	Mean number of days to germination	Number of seedlings that died (% of seedlings emerging)
Crataegus monogyna	1052	0 (0.0%)	-	-
Digitalis purpurea	1056	110 (10.4%)	65.5	10 (9.1%)
Hedera helix	1006	403 (40.1%)	14.0	57 (14.1%)
Prunella vulgaris	1081	427 (39.5%)	86.6	24 (5.6%)
Sorbus aucuparia	1071	0 (0.0%)	-	-
TOTAL	5266	940	-	91

4.3.2 Landscape cover and edge effects on seed germination in forest fragments

The field germination experiments revealed that germination success was much lower in forest fragments than in the laboratory for three species: 6.4% for *P. vulgaris* (77 seeds germinated), 3.0% for *D. purpurea* (169 germinated), and 2.6% for *H. helix* (7 germinated). In contrast, *S. aucuparia* germinated only under field conditions (21 germinated, 5.2% germination success). None of the *C. monogyna* seeds germinated during the 8-month field experiment. Although germination success was relatively low for all species, some of the species had significant responses to the landscape forest cover and distance from edge treatments (**Figure 4.2**).

Digitalis purpurea germination success was highest at the edge, especially in the 24% forest cover landscape, but in the 47% forest cover landscape it was highest 32 m from the edge (**Figure 4.2a**). The GLMs revealed that the Site x Plot interaction was highly significant for *D. purpurea* ($F_{8,60}$ = 6.074, p <0.001), meaning that differences in the proportion germinated among plots were much greater at some sites than others (see **Table 4.3**). Importantly, after accounting for the covariate effects of variation in soil pH and microclimate in the model, there was also a significant Landscape x Edgedist interaction effect on *D. purpurea* germination ($F_{1,5}$ = 34.162, p = 0.002, **Table 4.5**), indicating that the plot to plot, and site to site, variation in germination success was indeed directly related to both distance from the edge and percentage forest cover in the landscape. The significant Landscape x Edgedist interaction effect indicates that the slope of the distance from edge regression changed in relation to the amount of forest cover in the landscape – in this case the slope changed from negative in low forest cover landscapes to positive in higher forest cover landscapes (**Figure 4.2a**). The further addition of vegetation composition into the model removed the significance of the Landscape x Edgedist effect ($F_{1,4}$ = 0.785, p = 0.532, **Table 4.5**), suggesting that the composition of the resident plant community was responsible for explaining some of the Landscape x Edgedist regression effect on germination success.

Germination success of *P. vulgaris* was highest at fragment edges (with the exception of the 47% cover landscape), and there was a significant difference in mean proportion germinated among plots ($F_{2,8}$ = 5.103, p = 0.037, **Figure 4.2b**). The Site x Plot interaction was also significant ($F_{8,60}$ = 3.819, p = 0.001), again indicating that differences in germination among plots were greater at some fragments than others. The addition of covariates in the model improved the R^2 for the Landscape x Edgedist interaction, with microclimate producing the biggest increase (from 0.001 to 0.013), however the effect did not become significant ($F_{1,6}$ = 0.511, p = 0.502, **Table 4.5**).

Hedera helix germinated at three fragments only (in the 16%, 40% and 58% cover landscapes). Mean proportion germinated differed significantly among plots ($F_{2,8} = 5.112$, $p = 0.037$, **Table 4.5**), with germination success being highest in fragment interiors (**Figure 4.2c**). None of the treatment effects were significant, although the addition of microclimate improved the R^2 for the Landscape x Edgedist regression ($F_{1,6} = 0.973$, $p = 0.362$, **Table 4.5**). *Sorbus aucuparia* showed no clear response to the treatment effects, with germination success decreasing from edge to interior in three landscapes (24%, 40% and 58% forest cover), but having the opposite trend in the other two landscapes (**Figure 4.2d**). None of the treatment effects were significant, and the addition of covariates reduced the R^2 for the Landscape x Edgedist interaction (**Table 4.5**).

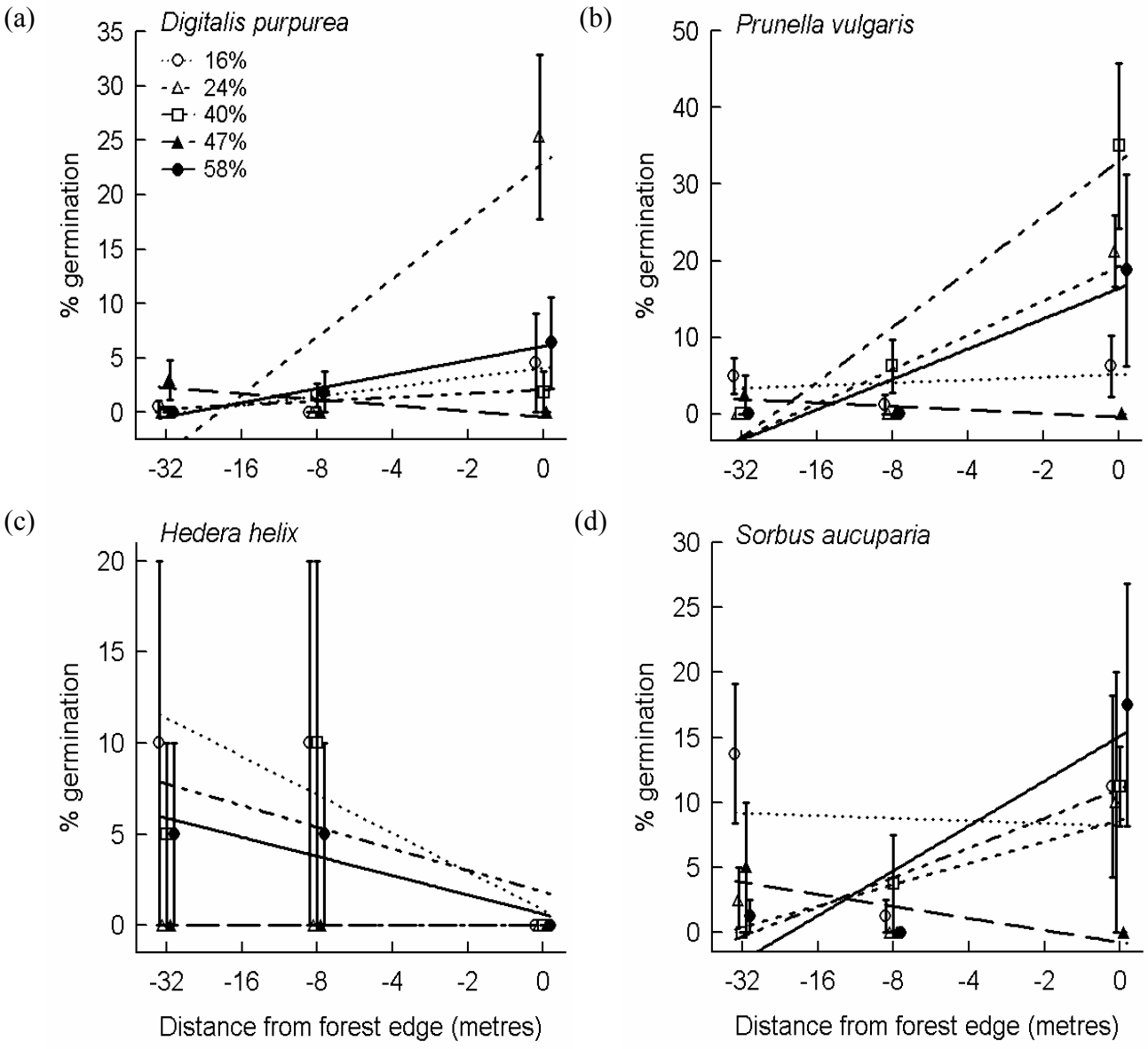


Figure 4.2. Mean percentage germination of (a) *Digitalis purpurea*, (b) *Prunella vulgaris*, (c) *Hedera helix*, and (d) *Sorbus aucuparia* seeds along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58%). The x-axis is on a log2 scale. Error bars indicate standard error. Linear regression lines are shown. Note: overlapping points are offset for clarity.

Table 4.5. Effects of environmental variables on the proportion germinated of *Digitalis purpurea*, *Prunella vulgaris*, *Hedera helix* and *Sorbus aucuparia* seeds in fragments in five landscapes. Treatment variables: **Landscape** = percentage native forest cover in the landscape, **Edgedist** = $\log_2$ distance from the forest edge, **Landscape x Edgedist** = Landscape x Edgedist interaction. Covariates: pH = soil pH; vegetation = Axis 1 of a DCA of plant species composition (<2 m in height); microclimate = Axis 1 scores from a PCA of percent canopy cover, mean daytime temperature, and mean daytime relative humidity. Best model = model with the largest R^2 for the Landscape x Edgedist interaction. The df, R^2, F- and P-values were taken from a composite ANOVA table created from the results of four separate GLMs with covariates added before the treatment variables (see Methods for details). Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*.

Generalised linear models (GLMs) with environmental covariates	**Landscape**				**Edgedist**				**Landscape x Edgedist**			
	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P
Digitalis purpurea												
Treatment-only model (T)	1,3	0.008	0.257	0.647	1,1	0.159	17.910	0.148	1,7	0.046	1.140	0.321
(best model) microclimate + pH + (T)	1,3	0.005	0.140	0.733	1,1	0.013	0.213	0.725	1,5	0.169	34.162	**0.002****
									model with all 3 covariates weakened Landscape x Edgedist effect			
vegetation + microclimate + pH + (T)	1,3	0.001	0.050	0.838	1,1	0.007	0.109	0.797	1,4	0.067	0.785	0.532
Prunella vulgaris												
Treatment-only model (T)	1,3	0.004	0.107	0.765	1,1	0.255	17.728	0.148	1,7	0.001	0.032	0.863
(best model) microclimate + (T)	1,3	0.003	0.255	0.648	1,1	0.012	0.785	0.538	1,6	0.013	0.511	0.502
									no more models were run as Landscape x Edgedist effect was not significant			
Hedera helix												
Treatment-only model (T)	1,3	0.002	0.087	0.787	1,1	0.036	6.946	0.231	1,7	0.001	0.191	0.675
(best model) microclimate + (T)	1,3	0.002	0.077	0.800	1,1	0.000	0.001	0.977	1,6	0.004	0.973	0.362
									no more models were run as Landscape x Edgedist effect was not significant			
Sorbus aucuparia												
Treatment-only model (T)	1,3	0.013	0.709	0.461	1,1	0.074	1.492	0.437	1,7	0.019	1.105	0.328
									all covariates weakened Landscape x Edgedist effect			
									no more models were run as Landscape x Edgedist effect was not significant			

4.3.3 Landscape cover and edge effects on seedling height growth in forest fragments

Almost all of the seedlings survived the field experiment (only 18 died out of 811 planted), and the mortality rate was very low for all three species: 2.7% for *D. purpurea*, 2.5% for *P. vulgaris*, and 1.8% for *H. helix*. The majority of seedlings increased in size and appeared quite healthy when harvested, however a few seedlings were showing signs of stress, with weak stems and blackened foliage. The maximum increase in height during the 8-month experiment was 1356 mm for *D. purpurea*, 718 mm for *P. vulgaris*, and 503 mm for *H. helix*. The three species showed differences in relative height growth in response to distance from the edge and forest cover in the landscape (**Figure 4.3**).

The average relative growth in height of *D. purpurea* seedlings varied significantly among plots ($F_{2,8} = 4.861$, $p = 0.042$) and was consistently higher at the edge in all landscapes, particularly in the 24% cover landscape (**Figure 4.3a**). The Landscape x Edgedist regression was significant in the Treatment-only model ($F_{1,7} = 8.207$, $p = 0.024$), and the addition of covariates (C/N ratio, phosphorus, pH, vegetation composition, nitrogen) strengthened the effect, with soil C/N ratio producing the biggest increase in the R^2 for the Landscape x Edgedist interaction (**Table 4.6**). In contrast, the Landscape x Edgedist interaction effect weakened when microclimate was added ahead of the treatment variables in the model (**Table 4.6**), which implies that microclimate explained some of the Landscape x Edgedist effect.

The Landscape x Edgedist regression had a highly significant effect on *P. vulgaris* relative height growth ($F_{1,15} = 21.580$, $p < 0.001$, **Table 4.6**). Seedlings planted in landscapes with low forest cover (16% and 24% cover) grew relatively larger at edges than fragment interiors, whereas seedlings in the higher forest cover landscapes (47% and 58% cover) grew more inside fragments than at edges (**Figure 4.3b**). The Landscape x Edgedist interaction effect was even more significant with soil pH and soil nitrogen included the model (**Table 4.6**). The addition of the remaining covariates in the model weakened the Landscape x Edgedist regression, implying that they explained some of the Landscape x Edgedist interaction effect, but the regression remained significant even with all six covariates included ($F_{1,9} = 9.873$, $p = 0.012$).

The relative height growth of *H. helix* seedlings increased significantly from the edge to interior in all landscapes (Edgedist regression $F_{1,3} = 14.901$, $p = 0.031$, **Table 4.6, Figure 4.3c**). The addition of pH in the model improved the R^2 for the Landscape x Edgedist regression slightly, but it remained non-significant (**Table 4.6**).

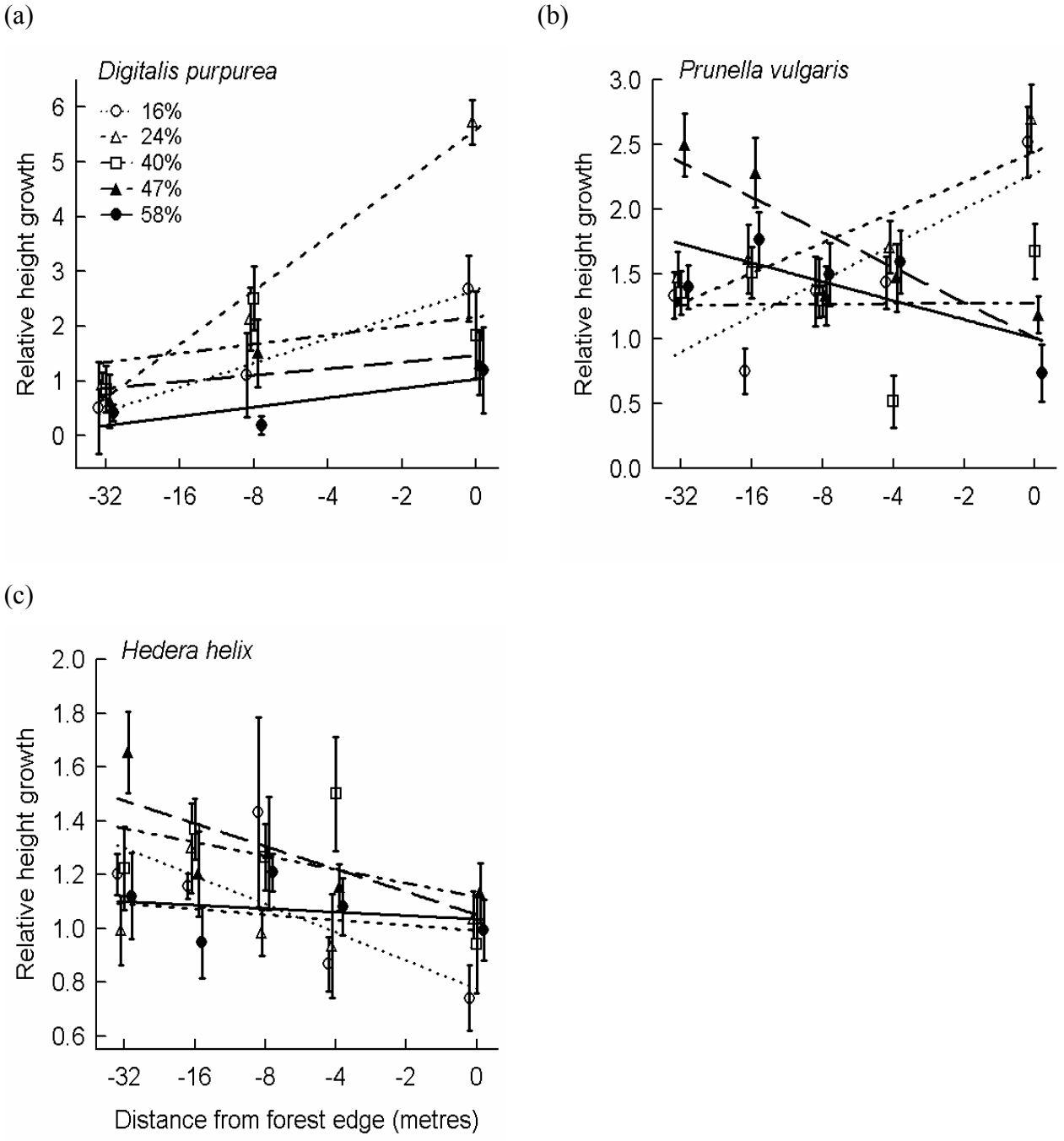


Figure 4.3. Mean relative growth in height of (a) *Digitalis purpurea*, (b) *Prunella vulgaris*, and (c) *Hedera helix* seedlings along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58%). The x-axis is on a log2 scale. Error bars indicate standard error. Linear regression lines are shown. Note: overlapping points are offset for clarity.

Table 4.6. Effects of environmental variables on the relative growth in height of *Digitalis purpurea*, *Prunella vulgaris* and *Hedera helix* seedlings in fragments in five landscapes. Treatment variables: **Landscape** = percentage native forest cover in the landscape, **Edgedist** = $\log_2$ distance from the forest edge, **Landscape x Edgedist** = Landscape x Edgedist interaction. Covariates: pH = soil pH; N = total soil nitrogen; P = available soil phosphorus; C/N = soil carbon to nitrogen ratio; vege = Axis 1 scores from a DCA of plant species composition (<2 m in height); climate = Axis 1 scores from a PCA of percent canopy cover, mean daytime temperature, and mean daytime relative humidity. Best model = model with the largest R^2 for the Landscape x Edgedist interaction. The df, R^2, F- and P-values were taken from a composite ANOVA table created from the results of four separate GLMs with covariates added before the treatment variables (see Methods for details). Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*.

Generalised linear models (GLMs) with environmental covariates	**Landscape**				**Edgedist**				**Landscape x Edgedist**			
	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P
Digitalis purpurea												
Treatment-only model (T)	1,3	0.081	2.772	0.195	1,1	0.129	7.301	0.226	1,7	0.065	8.207	**0.024***
C/N + (T)	1,3	0.067	2.262	0.230	1,1	0.129	5.127	0.265	1,6	0.077	13.309	**0.011***
vege + pH + P + C/N + (T)	1,3	0.028	1.298	0.337	1,1	0.057	2.590	0.354	1,3	0.088	14.157	**0.033***
(best model) N + vege + pH + P + C/N + (T)	1,3	0.001	0.035	0.864	1,1	0.023	1.494	0.437	1,2	0.089	10.441	0.084
									model with all 6 covariates weakened Landscape x Edgedist effect			
climate + N + vege + pH + P + C/N + (T)	1,3	0.000	0.004	0.953	1,1	0.011	0.384	0.647	1,1	0.074	7.290	0.226
Prunella vulgaris												
Treatment-only model (T)	1,3	0.003	0.218	0.672	1,3	0.001	0.146	0.728	1,15	0.150	21.580	**<0.001*****
(best model) N + pH + (T)	1,3	0.000	0.025	0.884	1,3	0.001	0.121	0.751	1,13	0.185	39.472	**<0.001*****
									all models with 3 or more covariates weakened Landscape x Edgedist effect			
vege + climate + P + C/N + N + pH + (T)	1,3	0.001	0.024	0.887	1,3	0.003	0.457	0.547	1,9	0.049	9.873	**0.012***
Hedera helix												
Treatment-only model (T)	1,3	0.004	0.398	0.573	1,3	0.027	14.901	**0.031***	1,15	0.003	0.584	0.457
(best model) P + (T)	1,3	0.001	0.131	0.741	1,3	0.022	12.199	**0.040***	1,14	0.004	0.713	0.413
									no more models were run as Landscape x Edgedist effect was not significant			

4.3.4 Landscape cover and edge effects on flowering by seedlings in forest fragments

Digitalis purpurea seedlings produced flowers in all five landscapes, and at all distances from the edge. The average number of flowers per seedling was highest at the edge, particularly in the landscape with 24% forest cover, where some seedlings had over 50 flowers per flower spike (**Figure 4.4a**). None of the treatment effects were significant in the Treatment-only model, but the addition of soil C/N ratio in the model resulted in a significant Landscape x Edgedist effect ($F_{1,6}$ = 16.332, p = 0.007, **Table 4.7**), implying that the C/N ratio had confounded the Landscape x Edgedist interaction effect on *D. purpurea* flower production. Microclimate and soil nitrogen also appeared to have confounding effects, as the R^2 for the Landscape x Edgedist interaction increased with these covariates in the model ($F_{1,4}$ = 45.904, p = 0.002, **Table 4.7**). The significant Landscape x Edgedist effect indicates that the slope of the distance from edge regression changed in relation to the amount of forest cover in the landscape – in this case the slope was steeper in low forest cover landscapes than in high forest cover landscapes (**Figure 4.4a**). The addition of the remaining covariates (soil pH, phosphorus, vegetation composition) weakened the Landscape x Edgedist interaction effect, and it became non-significant with all six covariates in the model (**Table 4.7**), suggesting that these variables had explained some of the Landscape x Edgedist effect.

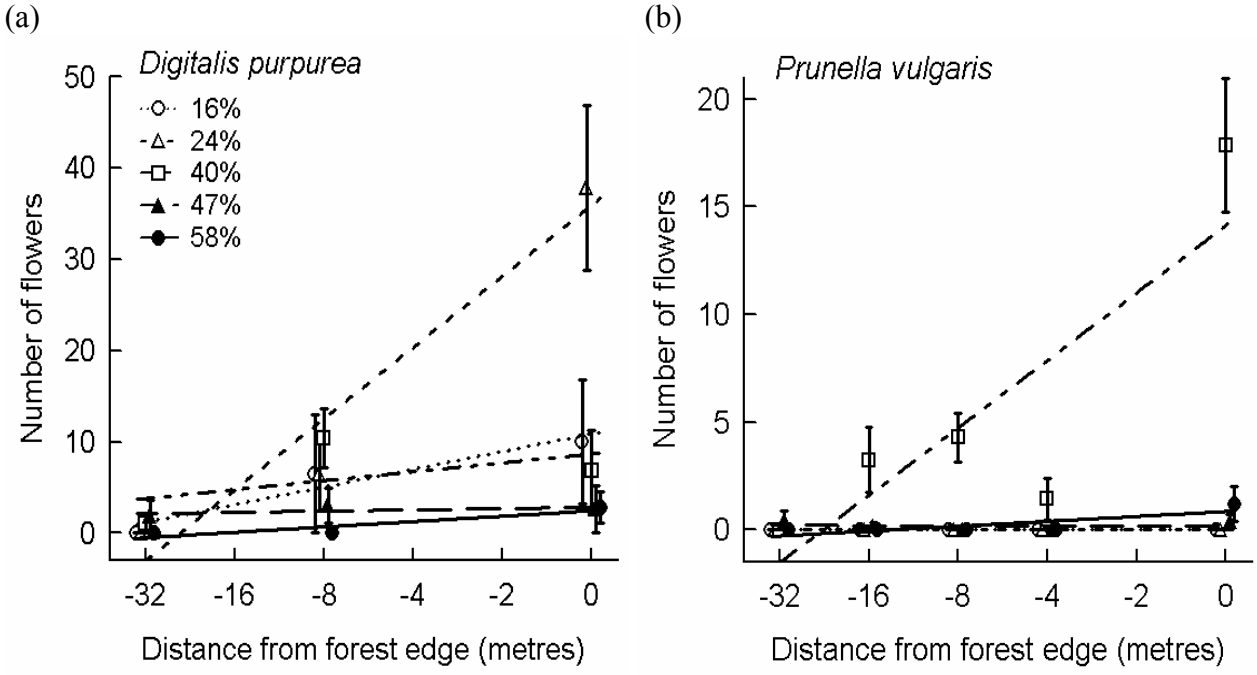


Figure 4.4. Mean number of flowers per (a) *Digitalis purpurea* and (b) *Prunella vulgaris* seedling along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58%). The x-axis is on a log2 scale. Error bars indicate standard error. Linear regression lines are shown. Note: overlapping points are offset for clarity.

Table 4.7. Effects of environmental variables on the number of flowers per *Digitalis purpurea* and *Prunella vulgaris* seedling in fragments in five landscapes. Treatment variables: **Landscape** = percentage native forest cover in the landscape, **Edgedist** = $\log_2$ distance from the forest edge, **Landscape x Edgedist** = Landscape x Edgedist interaction. Covariates: pH = soil pH; N = total soil nitrogen; P = available soil phosphorus; C/N = soil carbon to nitrogen ratio; vege = Axis 1 scores from a DCA of plant species composition (<2 m in height); climate = Axis 1 scores from a PCA of percent canopy cover, mean daytime temperature, and mean daytime relative humidity. Best model = model with the largest R^2 for the Landscape x Edgedist interaction. The df, R^2, F- and P-values were taken from a composite ANOVA table created from the results of four separate GLMs with covariates added before the treatment variables (see Methods for details). Significant effects are shown in bold: p <0.001***, p <0.01**, p <0.05*.

Generalised linear models (GLMs) with environmental covariates	**Landscape**				**Edgedist**				**Landscape x Edgedist**			
	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P
Digitalis purpurea												
Treatment-only model (T)	1,3	0.058	3.407	0.162	1,1	0.119	4.205	0.289	1,7	0.047	2.383	0.167
C/N + (T)	1,3	0.072	3.083	0.177	1,1	0.098	5.698	0.253	1,6	0.134	16.332	**0.007****
(best model) N + climate + C/N + (T)	1,3	0.015	0.470	0.542	1,1	0.008	11.164	0.185	1,4	0.149	45.904	**0.002****
	models with 4 or more covariates weakened Landscape x Edgedist effect											
pH + N + climate + C/N + (T)	1,3	0.004	0.138	0.735	1,1	0.005	8.325	0.212	1,3	0.136	36.092	**0.009****
vege + P + pH + N + climate + C/N + (T)	1,3	0.001	0.024	0.886	1,1	0.010	1.242	0.466	1,1	0.127	42.959	0.096
Prunella vulgaris												
Treatment-only model (T)	1,3	0.012	0.110	0.762	1,3	0.074	13.986	**0.033***	1,15	0.014	0.824	0.378
(best model) pH + (T)	1,3	0.003	0.042	0.851	1,3	0.051	9.748	0.052	1,14	0.016	0.875	0.365
	no more models were run as Landscape x Edgedist effect was not significant											

Prunella vulgaris seedlings produced flowers only in landscapes with relatively high forest cover (40%, 47% and 58% forest cover) (**Figure 4.4b**). The average number of flowers per seedling differed significantly between Sites ($F_{4,16} = 4.795$, $p = 0.010$), with seedlings in the 40% landscape producing the most flowers (**Figure 4.4b**). The mean number of flowers decreased with distance from the forest edge, resulting in a significant Edgedist regression ($F_{1,3} = 13.986$, $p = 0.033$, **Table 4.7**). The addition of covariates in the model improved the Landscape x Edgedist regression, however it did not become significant, therefore no more models were run (**Table 4.7**). In contrast, the addition of covariates weakened the Edgedist regression, and the effect became non-significant with soil pH included in the model (**Table 4.7**), suggesting that the covariates explained some of the Edgedist effect.

4.3.5 Variation in environmental covariates among plots and sites

Edge gradients in microclimate showed broadly similar trends in all landscapes (**Figure 4.5**). Mean daytime temperatures (between 8 am and 7 pm) ranged from 21.2°C at the edge to 11.4°C in plots 32 m inside the forest. Temperatures in the two landscapes near Lake Brunner (16% and 47% forest cover landscapes) were consistently lower than those in the Grey and Waipuna Valleys (**Figure 4.5a**). Mean daytime relative humidity ranged from 76.4% at the edge to 97.1% 32 m inside the forest, and was lowest in the 16% cover landscape (**Figure 4.5b**). Percentage canopy cover increased inside fragments with distance from the edge, and was generally highest in the two higher forest cover landscapes (47% and 58% forest cover) (**Figure 4.5c**).

In contrast to the microclimatic variables, soil characteristics varied widely between sites and plots, and there were no consistent changes with distance from the edge (**Figure 4.6**). Soil pH ranged from 3.8 in the 16% cover landscape to a maximum of 5.0 at the edge in the 40% forest cover landscape (**Figure 4.6a**). Total soil nitrogen was lowest in the 24% and 40% cover landscapes (**Figure 4.6b**), and decreased from the edge to interior in the 16% cover landscape, but showed the opposite trend in the 58% forest cover landscape. Phosphorus levels at fragment edges appeared to align with the proportion of forest cover in the landscape, as available phosphorus concentration increased with decreasing landscape forest cover (**Figure 4.6c**). Phosphorus levels within fragments were variable among sites, however, and did not appear to correspond to forest cover in the landscape. The C/N ratio was consistently highest in the 40% forest cover landscape and lowest in the 24% forest cover landscape, and showed a marked decrease from the edge to interior in the 58% forest cover landscape (**Figure 4.6d**).

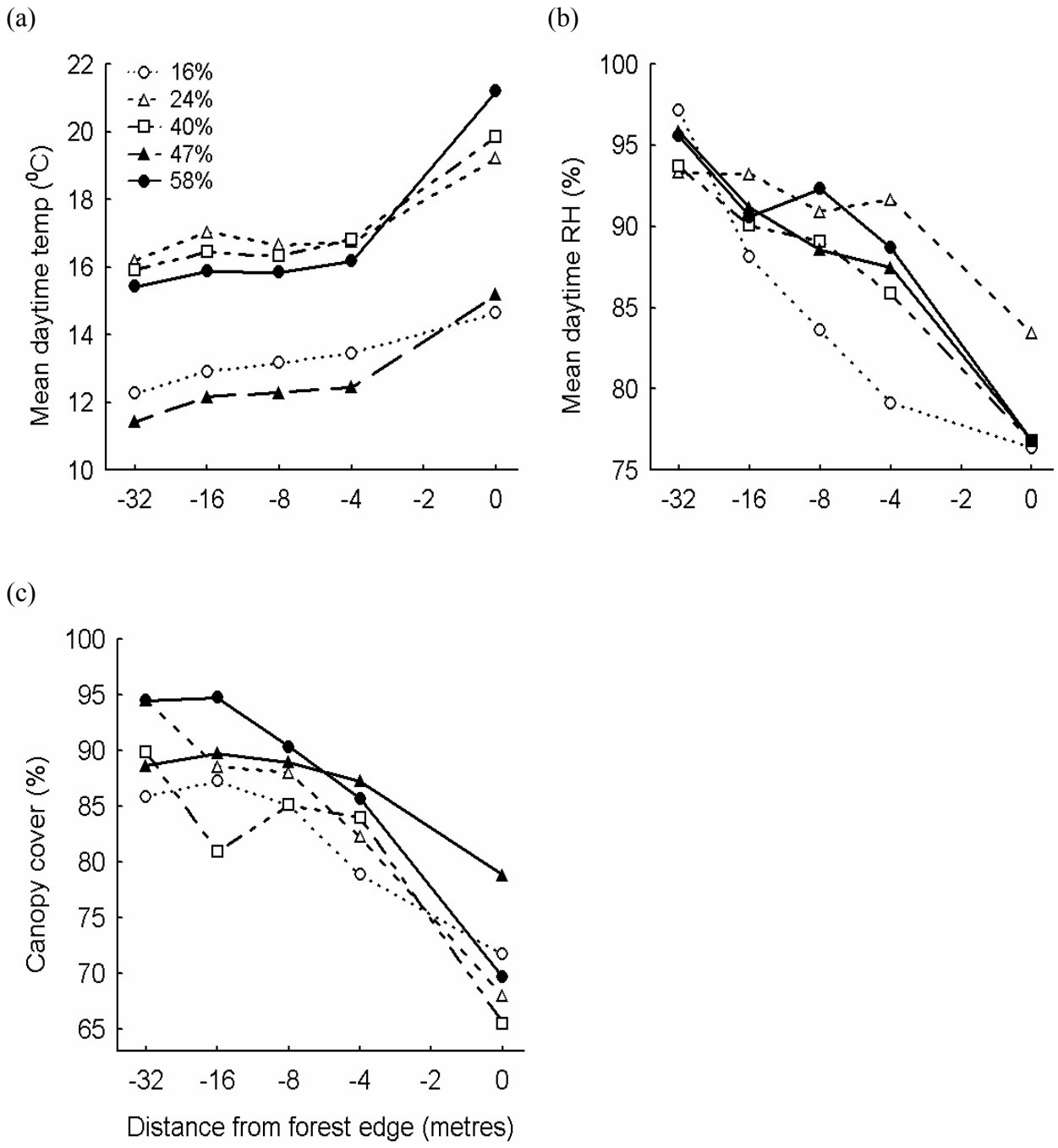


Figure 4.5. Variation in microclimate – (a) mean daytime temperature (°C), (b) daytime relative humidity (%) and (c) canopy cover (%) – along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58%). The x-axis is on a log2 scale. Error bars were too small to show.

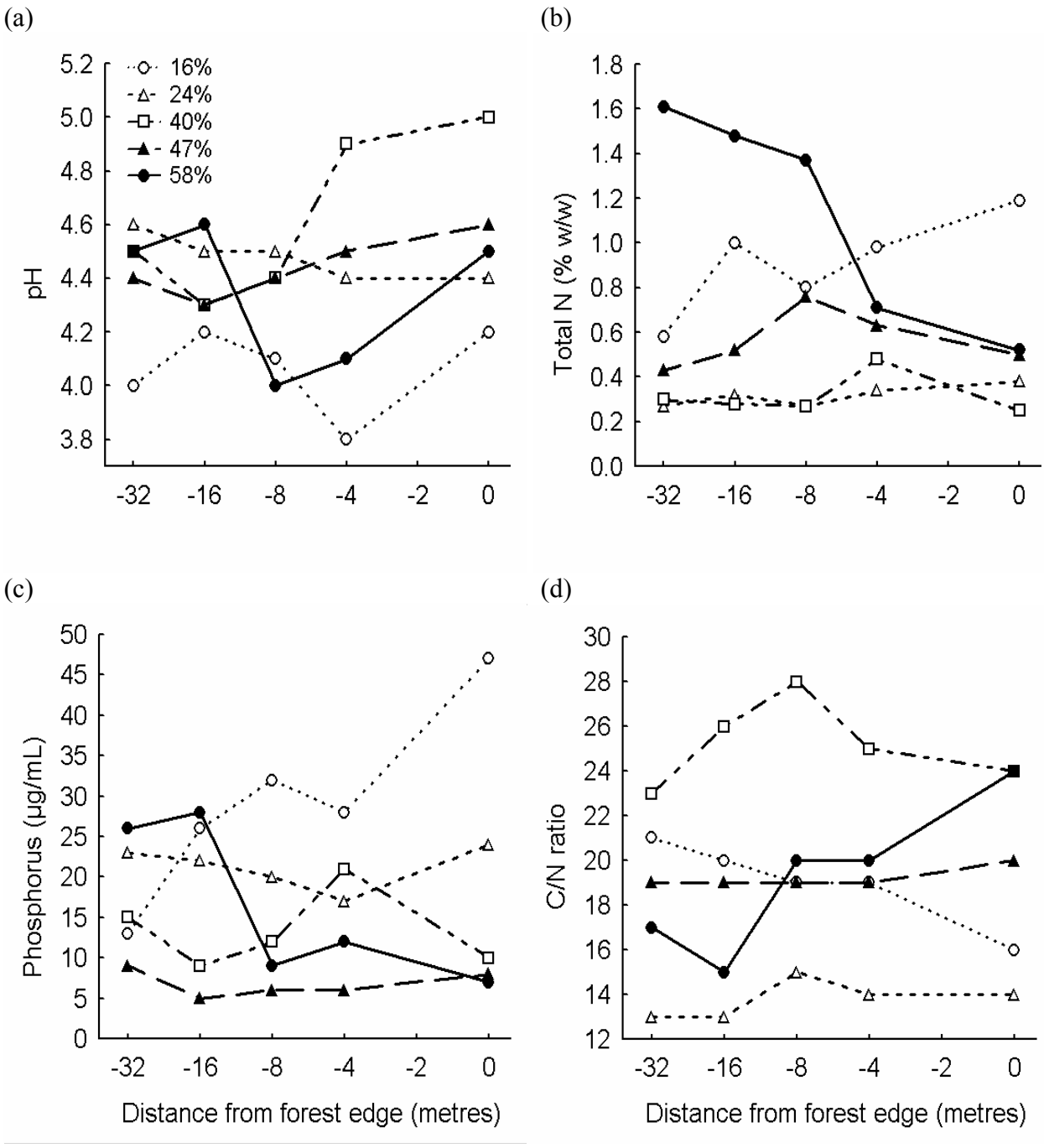


Figure 4.6. Variation in soil characteristics – (a) pH, (b) total nitrogen, (c) available phosphorus and (d) carbon to nitrogen ratio – along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58%). The x-axis is on a log2 scale.

In total, 166 vascular plant species were recorded in the vegetation plots, comprising 128 native and 38 exotic species. The most commonly recorded species were *Coprosma tayloriae* (in 29 plots), *Asplenium flaccidum* (28 plots), *Neomyrtus pedunculata* (26 plots) and *Myrsine divaricata* (25 plots). Detrended correspondence analysis (DCA) revealed that the 24% forest cover landscape had different plant species composition from the other landscapes, as it was separated from them along Axis 1 (**Figure 4.7**). DCA axis 1 (which explained 16.3% of the variation in the species data) was strongly positively correlated with the ferns *Grammitis billiardieri*, *Cyathea smithii, Dicksonia fibrosa* and *Hymenophyllum villosum,* and negatively correlated with *Coprosma rotundifolia*, *Cardamine debilis, Polystichum vestitum, Aristotelia serrata* and *Digitalis purpurea*. Species in the latter group, including the exotic *D. purpurea*, are commonly found in disturbed or early successional forest (pers. obs.). Fragments in the higher forest cover landscapes (47% and 58% forest cover) were separated from the others along DCA axis 2 (which explained 8.5% of the variation). This was mainly because of the presence of *Dacrycarpus dacrydioides* (a canopy tree) in these two landscapes, and the understorey species *Microlaena avenacea* and *Blechnum novae-zelandiae*. All landscapes showed a change in species composition along the edge gradient, however there was relatively little species turnover among plots in the 40% forest cover landscape.

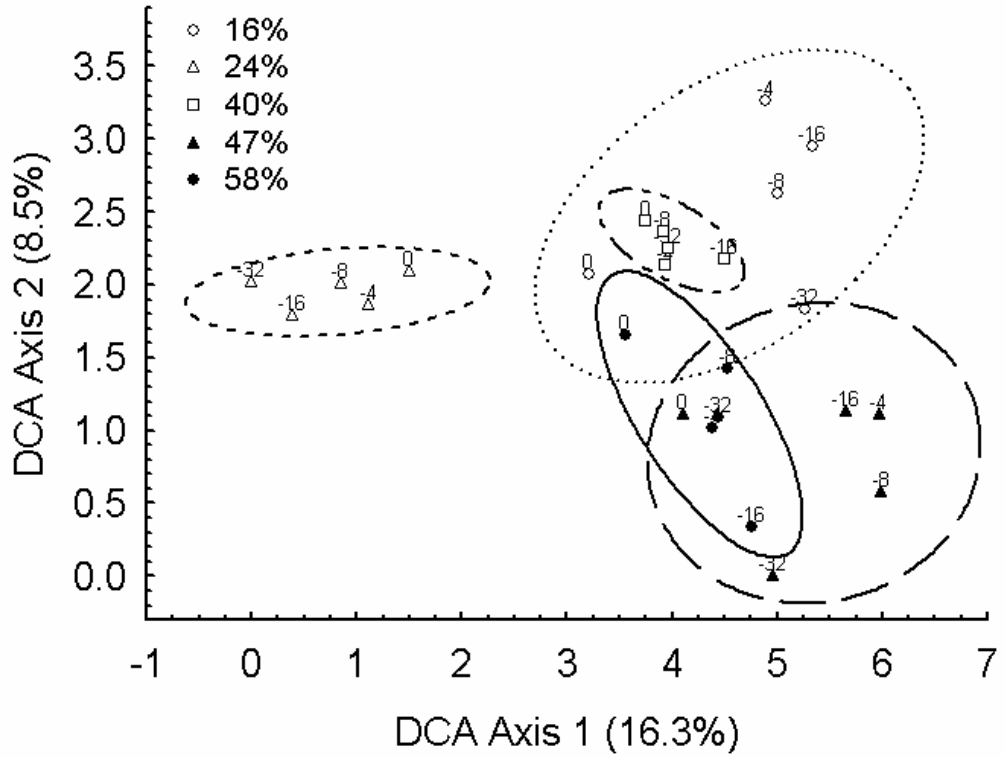


Figure 4.7. Detrended correspondence analysis (DCA) of vascular plant species composition in each plot (<2 m in height) along edge gradients in five landscapes with varying percentages of native forest cover (16%, 24%, 40%, 47%, and 58% forest cover). The first axis explained 16.3% of the variation in the species data, and the second axis explained a further 8.5%. Point labels show log2 distance from the forest edge: -0, -4, -8, -16, and -32 m.

4.4 DISCUSSION

4.4.1 Interactions between landscape cover and edge effects on plant responses

The propagule addition experiments revealed significant interaction effects between the amount of forest cover in the landscape and invasion success at forest edges. Edge gradients in germination, growth and flowering of some species were strongest in forest fragments located in more heavily deforested landscapes, suggesting that fragments in these landscapes may be more vulnerable to invasion. Plant species varied in their responses to the treatment variables, however, with the landscape forest cover by distance from edge interaction effect only observed for the two herbaceous, short-lived species with unspecialised dispersal mechanisms (*Digitalis purpurea* and *Prunella vulgaris*). Not surprisingly, fragment edges appear to provide the most favourable conditions for germination, growth and reproduction of these species, but in addition, edges in landscapes with less forest cover appear to be particularly invasible. By contrast, of the three woody, bird-dispersed perennials (*Hedera helix*, *Sorbus aucuparia* and *Crataegus monogyna*), only *H. helix* showed a significant response to the edge gradient, with higher germination and growth rates towards the forest interior; and none of these species showed a significant response to the proportion of forest cover in the landscape.

4.4.2 Traits affecting germination and growth responses of exotic plants

The differing responses of the two functional groups to landscape cover and edge effects suggest that some plant traits may be more advantageous in highly fragmented landscapes. Forest fragments in heavily deforested landscapes are likely to be more modified and disturbed than those in more intact landscapes, resulting in higher light, temperature, and nutrient levels, particularly at forest edges (With 2004; Fischer & Lindenmayer 2007). *Digitalis purpurea* germination is known to increase with light availability and temperature, and is promoted by soil disturbance (van Baalen 1982), therefore these conditions are likely to promote invasion by *D. purpurea*. *Prunella vulgaris* shares similar traits to *D. purpurea*, so *P. vulgaris* is also likely to be more invasive at disturbed fragment edges in highly modified landscapes.

In contrast, *H. helix* performed poorly at forest edges, and had the lowest overall germination and growth rates of any species. *H. helix* had the highest seedling survival rate, however, suggesting that its strategy for invading forest habitats may be to persist and spread vegetatively rather than rely on fast germination and growth. *Hedera helix* germination is known to be inhibited by light

(Metcalfe 2005), and the higher light intensity at edges (in combination with higher temperatures and lower relative humidity) appears to have prevented germination at fragment edges. Conditions at edges also appear to be less favourable for growth of *H. helix* seedlings, as growth rates were higher inside forest fragments. *Hedera helix* is considered to be highly shade-tolerant (Laskurain *et al.* 2004), and *H. helix* seedlings are able to establish in understorey conditions with evergreen shade, as they have a relatively low light compensation point (Metcalfe 2005). *Hedera helix* appears to grow "most vigorously in shaded, moist sites on heavy, fertile soils" (Metcalfe 2005), so not surprisingly, conditions in forest fragments on the West Coast appear to be quite suitable for *H. helix* germination and growth. *Sorbus aucuparia* is also considered to have high shade-tolerance, as seeds can germinate and establish under low light conditions in dense forest stands (Zerbe 2001). *Sorbus aucuparia* did not respond clearly to landscape or edge effects, however, and I could not determine seedling growth responses, as no seedlings were available (*S. aucuparia* seeds failed to germinate under laboratory conditions). *Sorbus aucuparia* seeds require cold stratification to break embryo and seed coat dormancy (Raspé *et al.* 2000), and it appears that *S. aucuparia* seeds may have needed a longer stratification period in the field to induce germination.

4.4.3 Environmental covariates affecting plant responses

A number of the environmental covariates appeared to have important effects on germination, growth and flowering rates of exotic plants in forest fragments. Microclimate explained part of the landscape forest cover by distance from edge interaction effect on *D. purpurea* and *P. vulgaris* relative height growth, suggesting that differences in temperature, relative humidity and/or light availability may have been partly driving seedling growth responses at fragment edges. Canopy cover tended to be lower in fragments in more heavily deforested landscapes, which implies that native tree species in these fragments may have been negatively affected by a higher degree of modification and disturbance in these landscapes.

Several of the soil variables had an important influence on the significance of the treatment effects, even though the experiments were carried out using standardised potting mix, which would have tended to reduce the effects of natural soil conditions on plant responses. Available phosphorus levels were higher at fragment edges in landscapes with low native forest cover, and appeared to partly explain the significant landscape cover by edge effects on *D. purpurea* growth and *P. vulgaris* flower production. Phosphorus is an essential plant nutrient that has previously been linked with the invasion of exotic plants into forest remnants (Wiser *et al.* 1998; Allcock 2002; King & Buckney 2002; Chabrerie *et al.* 2008). Phosphorus levels may be elevated at

fragment edges in heavily deforested landscapes because of higher fertiliser use on farmland (particularly superphosphate) in the surrounding landscape (Stevenson 2004), and/or because of higher natural soil fertility in these landscapes prior to fragmentation (Lindenmayer & Luck 2005). The C/N ratio appeared to be important for explaining some of the landscape cover by edge interaction effect on *P. vulgaris* growth, suggesting that the availability of nitrogen in the soil may have been important for the growth of *P. vulgaris* seedlings (Russell 1973). Soil pH and nitrogen levels were very variable between plots, and did not appear to be related to the amount of native forest cover in the landscape. Consequently, pH and total nitrogen were confounding factors in detecting landscape forest cover by distance from edge interaction effects on *P. vulgaris* height growth, and *D. purpurea* germination, growth, and flower production. However, soil pH was noticeably higher at the edge in the 40% forest cover landscape, and *P. vulgaris* had the highest germination, growth and flowering rates in these plots, which implies that *P. vulgaris* may perform better on less acidic soils.

Vegetation composition appeared to be an important factor explaining the significant landscape forest cover by edge distance interaction effect on *D. purpurea* responses. Germination, growth and flowering rates of *D. purpurea* were markedly higher in the 24% forest cover landscape, and the ordination revealed that the plant community at this site was quite different from the other sites. The vegetation in the 24% cover landscape was characterised by a number of plant species that are found in disturbed or successional forest, including *D. purpurea*, which indicates that *D. purpurea* performed particularly well in a landscape where it occurred naturally at higher abundance. The 24% cover landscape also had the lowest soil C/N ratio (i.e. highest N availability) and higher daytime relative humidity levels than most other sites, suggesting that this landscape had different environmental characteristics from the other landscapes, and that this may have been responsible for the significant interaction effect, irrespective of forest cover in the landscape.

Other factors that were not measured in my study may have also influenced plant responses to landscape cover and edge gradients. Soil moisture, for example, is likely to have a strong effect on the germination, growth and reproduction of most plant species (Meekins & McCarthy 2001). Soil biota are also known to influence plant establishment, and can have both positive and negative effects on plants through a number of mechanisms, such as pathogenic effects, mycorrhizal fungus mutualisms, and alteration of nutrient cycles (Callaway *et al.* 2004b). The presence of exotic soil microbes has been linked with the invasion of exotic plant species in several other studies (Richardson *et al.* 2000a; Callaway *et al.* 2004a; Niu *et al.* 2007). Exotic soil biota may be more common in highly modified landscapes as a result of human activities, and this may further

promote the invasion of exotic plants in these landscapes. The presence of fungal pathogens and insect herbivores may have also affected plant growth responses in this study (Keane & Crawley 2002; Callaway & Maron 2006).

4.4.4 Factors limiting invasions of exotic plants in forest fragments

Germination appears to be the main stage limiting establishment of exotic plants in native forest fragments, as germination success was very low for all species. Seedling survival was very high during the eight-month experiment, however, which suggests that once established, exotic plant species could persist for some time inside forest fragments. In addition, flower production by the two shorter-lived species suggests that population increase and further spread is also possible. Although germination and growth rates may have been lower if propagules had been planted in natural soils, the experiments demonstrated that exotic species from two contrasting functional groups were able to germinate and grow under a range of natural conditions in native forest fragments on the West Coast. Invasions of some species at forest edges and further population increase could eventually allow invasion into fragment interiors, as increased propagule pressure could over-ride the low invasibility of fragments for these species (Richardson & Pysek 2006). Control of exotic plants at edges could therefore play a key role in reducing invasions into fragments (Brothers & Spingarn 1992; Cadenasso & Pickett 2001).

Forest interior habitats were less favourable than fragment edges, particularly in high forest cover landscapes, for short-lived herbaceous species such as *D. purpurea* and *P. vulgaris*. This suggests that fragments in these landscapes had lower invasibility for these species, and that habitat suitability may be limiting their invasion into these fragments. In contrast, the invasion of long-lived, shade-tolerant species such as *H. helix* into forest fragments seems likely to be limited more by propagule availability, as germination and growth rates were highest in forest interiors, and landscape cover had no apparent effect on plant responses. I acknowledge that these observations are based on a limited number of sites and species, however, and that other factors not considered in this study could have influenced plant responses. Further research is needed to evaluate the relative importance of propagule pressure and landscape context in driving invasions of different species in native forest fragments, and to determine the extent to which propagule pressure can compensate for low community invasibility (Richardson & Pysek 2006). Long-term propagule addition experiments with variable numbers of seeds and seedlings would improve our understanding of these factors, and allow us to determine what level of propagule pressure is necessary for invasion of exotic plants into native forest fragments.

Chapter 5 – Differential responses of native plants to edge and area effects in forest fragments: the importance of life history traits

5.1 INTRODUCTION

Habitat fragmentation has major impacts on native plant communities, and these occur across a range of spatial and temporal scales (Collinge 1996; Debinski & Holt 2000; Honnay *et al.* 2005; Ewers & Didham 2006a). Two of the most important effects of forest fragmentation are the creation of abrupt habitat boundaries (edges) and the reduction in habitat area (Murcia 1995; Collinge 1996). Firstly, altered abiotic conditions at forest edges can lead to dramatic changes in plant communities, including changes in species composition and seedling recruitment patterns, lower tree basal areas, and increases in the densities of lianes and successional trees, which are collectively referred to as "edge effects" (Williams-Linera 1990; Brothers & Spingarn 1992; Chen *et al.* 1992; Laurance *et al.* 1998a; Laurance *et al.* 1998b; Fagan *et al.* 1999; Mesquita *et al.* 1999; Sizer & Tanner 1999; Laurance *et al.* 2001; Benítez-Malvido & Martínez-Ramos 2003; Harper *et al.* 2005; Laurance *et al.* 2006). Flower production, pollination and dispersal rates may increase or decrease at edges, and this will have a major effect on fruit and seed set, and ultimately population viability (Jules & Rathcke 1999; Kollmann & Schneider 1999; Cunningham 2000; Hobbs & Yates 2003; Montgomery *et al.* 2003; Honnay *et al.* 2005).

Secondly, forest fragmentation results in a reduction in the area of habitat available for forest-interior species, as well as increased isolation of forest fragments (Grashof-Bokdam 1997; Jacquemyn *et al.* 2001b). Smaller fragments are expected to support smaller populations, which are at higher risk of stochastic extinction, resulting in fewer species (MacArthur & Wilson 1967; Hanski & Gilpin 1991; Burkey 1995). Individuals from small populations may also have lower reproductive output, leading to further population decline (Young *et al.* 1996; Jacquemyn *et al.* 2002; Honnay *et al.* 2005). In addition to the spatial effects of small size and isolation, small fragments are also likely to experience higher levels of disturbance (e.g. grazing, logging, wind-throw, fire, drainage, nutrient enrichment) than larger areas of forest (Janzen 1983; Saunders *et al.* 1991; Hobbs 1993; Kemper *et al.* 1999; Gascon *et al.* 2000; Hobbs 2001; Echeverría *et al.* 2007), which may lead to substantial long-term changes in plant species composition. For example, grazing can have major effects on plant species composition in forest fragments, because some species are more accessible and palatable than others to herbivores (Yates *et al.* 2000; Kirby 2001; Smale *et al.* 2005). Species in small fragments are also likely to be subject to the effects of

agricultural chemicals such as pesticides, herbicides and fertilizers which may drift from surrounding farmland (Weathers *et al.* 2001; Stevenson 2004; Duncan *et al.* 2008).

Edge and area effects have been shown to vary among plant species with different growth forms and in different vegetation tiers within forest fragments (Malcolm 1994; Harper & MacDonald 2001). For example, a study in Amazonian forest fragments found varying penetration of edge effects in different vegetation tiers – a reduction in foliage density was detected up to 60 m from the edge in the canopy, but only up to 35 m in understorey vegetation (Malcolm 1994). Another study on the woody flora of forest fragments in Mexico revealed that the species richness of shrubs and understorey trees varied significantly with fragment area, shape and isolation, whereas the species richness of canopy trees was not related to any fragmentation variables (Ochoa-Gaona *et al.* 2004). One explanation for this is that long-lived species such as trees, could take decades or even centuries to respond to reduced habitat area – a situation referred to as an 'extinction debt' (Tilman *et al.* 1994; Brooks *et al.* 1999; Hanski & Ovaskainen 2002; Honnay *et al.* 2005). In these cases, species diversity may be more closely related to historical, rather than current, fragment and landscape configuration (Lindborg & Eriksson 2004; Snall *et al.* 2004; Honnay *et al.* 2005; Helm *et al.* 2006). In general, short-lived, fast-growing species such as herbaceous dicotyledons and ferns are likely to react faster to land use change faster than long-lived, slow-reproducing perennials, which may take decades or centuries to respond to fragmentation effects (van Ruremonde & Kalkhoven 1991; Turner *et al.* 1996; Lindborg 2007).

Although most studies show that the majority of forest-dwelling species are likely to be negatively affected by forest fragmentation (referred to as "forest specialists"), some species appear to be unaffected or respond positively to edge and area effects ("edge-positive" or "fragmentation-positive" taxa) (Grashof-Bokdam 1997; Bender *et al.* 1998; Harper & MacDonald 2001; Laurance *et al.* 2002). As recent studies have emphasised, life history traits play a key role in determining native plant responses to edge and area effects, and will therefore influence whether species are able to survive following fragmentation (Jacquemyn *et al.* 2001b; Godefroid & Koedam 2003; Jacquemyn *et al.* 2003; Zhu *et al.* 2004; Herault & Honnay 2005; Kolb & Diekmann 2005; Aguilar *et al.* 2006; Baldwin & Bradfield 2007; Lindborg 2007). Traits considered by other studies include: life form, longevity, dispersal mechanism, self-compatibility, seed number, seed mass, seed longevity (formation of seed banks) and clonal ability (Dupré & Ehrlén 2002; Jacquemyn *et al.* 2003; Maurer *et al.* 2003; Kolb & Diekmann 2005; Piessens *et al.* 2005; Baldwin & Bradfield 2007; Lindborg 2007; Van der Veken *et al.* 2007; Aparicio *et al.* 2008). Traits such as high dispersal ability or persistence in the seed bank are likely to reduce the risks of

local population extinction in fragments (Piessens *et al.* 2005; Lindborg 2007). Having generalist habitat requirements and the ability to use secondary habitats in the matrix will also minimise the impacts of forest fragmentation (Bender *et al.* 1998; Laurance *et al.* 2002; Debinski 2006; Kupfer *et al.* 2006). In contrast, specialist forest-interior species are likely to be at greater risk of extinction as a result of fragmentation than generalists, because of their specific habitat requirements, low dispersal power, and inability to move between isolated fragments (Jacquemyn *et al.* 2001a; Dupré & Ehrlén 2002; Honnay *et al.* 2005; Kolb & Diekmann 2005; Baldwin & Bradfield 2007).

Dispersal mechanism appears to be a key trait affecting vulnerability to fragmentation, as it affects the ability of a plant species to move between fragments, and therefore the likelihood of metapopulation survival (Dupré & Ehrlén 2002; Verheyen *et al.* 2004). In the case of animal-dispersed species, interactions with dispersers will have a major influence on plant population dynamics, as populations of some animal mutualists may be reduced by fragmentation, resulting in lower seed production, viability, and seedling survival of plant species which depend on them (Clout & Hay 1989; Kremen & Ricketts 2000; Cordeiro & Howe 2001; Lennartsson 2002; Hobbs & Yates 2003; Garcia & Chacoff 2007). In contrast, plants with abiotic long-distance dispersal mechanisms (e.g. anemochory, hydrochory) are likely to be less vulnerable to reduced fragment area and isolation (Matlack 1994a; Grashof-Bokdam 1997; Tabarelli *et al.* 1999). For example, a study in fragmented forests in southern Sweden found that animal-dispersed species were more negatively affected by small fragment size than species with wind or unspecialised dispersal mechanisms (Dupré & Ehrlén 2002). Similarly, a study on seed dispersal among forest fragments in Michigan, USA found that animal-dispersed species had lower seed arrival rates in traps than wind-dispersed species (McEuen & Curran 2004). Another study on the reproductive ability of native shrubs in New Zealand revealed that insect-pollinated species were ranked higher in an assessment of vulnerability to fragmentation compared with wind-pollinated species (Merrett *et al.* 2007).

A number of studies have reported positive species-area relationships for plants in fragmented forests (e.g. Peterken & Game 1984; Grashof-Bokdam 1997; Honnay *et al.* 1999; Hill & Curran 2001; Benítez-Malvido & Martínez-Ramos 2003; Petit *et al.* 2004), whereas others have found a weak or no relationship between area and species richness (Kelly *et al.* 1989; Pärtel & Zobel 1999; Krauss *et al.* 2004; Helm *et al.* 2006). As recent trait-based studies have emphasised, different species or functional groups within a community may have conflicting responses to fragmentation (Jacquemyn *et al.* 2001b, 2003; Herault & Honnay 2005; Kolb & Diekmann 2005;

Baldwin & Bradfield 2007; Lindborg 2007), therefore lumping the entire community together may confound the detection of fragmentation effects (Ewers & Didham 2006a). For this reason, it is essential to analyse different functional groups separately in order to understand community responses to fragmentation (Herault & Honnay 2005).

The vast majority of research on the effects of forest fragmentation on plant communities has taken place in temperate forests in the Northern Hemisphere (e.g. Chen *et al.* 1992; Matlack 1994b; Grashof-Bokdam 1997; e.g. Meiners & Pickett 1999; Jacquemyn *et al.* 2001b; Petit *et al.* 2004; Kolb & Diekmann 2005; Guirado *et al.* 2006; Vellend *et al.* 2006) or tropical forests in Central and South America (e.g. Lovejoy *et al.* 1989; Didham & Lawton 1999; Laurance *et al.* 2002; Benítez-Malvido & Martínez-Ramos 2003; Broadbent *et al.* 2008). Forest loss has also been severe in most temperate Southern Hemisphere countries such as Chile (Echeverria *et al.* 2006) and New Zealand (Ewers *et al.* 2006), but there has been surprisingly little research on the impacts of forest fragmentation on plant communities in these countries (Echeverría *et al.* 2007). Prior to human settlement, the New Zealand archipelago was almost entirely covered in temperate forest (McGlone 1989; Leathwick 2001), but over the last 800 years Polynesian and European colonists have been responsible for the destruction of over 70% of the original vegetation cover (Wilmshurst *et al.* 2008). Currently less than 24% native forest cover remains, and the majority occurs in steep, high rainfall areas, at high altitudes (Leathwick *et al.* 2003b; Ewers *et al.* 2006). New Zealand has a relatively small number of native vascular plant species (approximately 2400 species), but a large proportion (>80%) of these are endemic (Wardle 1991; Lee *et al.* 2001). The native flora is dominated by long-lived woody perennials, ferns, and bryophytes, and is notable because of the prevalence of distinct, varied juvenile growth forms, and the relatively high level of dioecism (Dawson 1993). At low altitudes, the majority of native species may be considered forest and shrubland specialists (Wardle 1991), however forest edges are an important habitat for some native plants, such as non-woody species and shrubs (Merrett *et al.* 2007). Despite the severity of deforestation and high potential for significant impacts on the native flora, only a handful of studies have examined the effects of habitat loss and fragmentation on native plant communities in New Zealand (Young & Mitchell 1994; Norton 2002; Ohlemüller 2003; Miller *et al.* 2004; Bach *et al.* 2005; Smale *et al.* 2005).

The aim of my study was to investigate the effects of fragmentation on native plant communities in forest fragments on the West Coast of New Zealand, and to examine whether responses to fragmentation vary among different groups within these plant communities. I chose to focus on the effects of fragmentation at two spatial scales: variation among forest fragments of varying

area, and variation within fragments at differing distances from the edge. Firstly, I expected that fragment edges would be less suitable than interior habitats for the majority of native forest plants in my study area, leading to a reduction in native species richness at fragment edges. Secondly, I predicted that small fragments would have altered community composition and lower native species richness compared to large fragments. Because the effects of fragmentation may vary spatially within forest communities, I examined the strength of edge and area effects on species composition separately for different vegetation tiers. As life history traits are expected to play an important role in driving species responses to fragmentation, edge and area effects were examined separately for different groups of species according to two important axes of life history variation in plants: life form and dispersal mechanism. Based on the findings of previous trait-based studies, I predicted that (1) area effects would be stronger for short-lived life forms (e.g. herbaceous dicotyledons) than long-lived life forms (e.g. trees), (2) edge effects would be weakest for life forms that have generalist habitat requirements and can occupy matrix habitats, and (3) species dispersed by animals would be more negatively affected by forest fragmentation than species with abiotic or unspecialised dispersal mechanisms because of reduced dispersal rates in fragmented landscapes.

5.2 METHODS

5.2.1 Study area

The study was carried out in the Grey and Buller Districts on the West Coast of the South Island of New Zealand (42°08' to 42°36' and 171°25' to 171°46'). See **Chapter 2, section 2.2.1** for a full description of the study area, and **Figure 2.1** for a map.

5.2.2 Landscape and fragment selection

The study was conducted in 44 native forest fragments, which ranged in size from 0.3 to 330 ha. A geographic information system (GIS) analysis of the New Zealand Land Cover database (MfE 2004) was used to select 11 landscapes which ranged in native forest cover from 19.8% to 47.9%. Within each landscape, one native forest fragment was selected in each of four different size categories: 0.5-2.0 ha, 2.0-8.0 ha, 8.0-32.0 ha and >32.0 ha (see **Table 2.1** for a list of landscapes and fragments). See **Chapter 2, section 2.2.2** for a full description of the methods used to select landscapes and fragments. Note that data from the two Control landscapes (Forest Control and

Matrix Control) were not used in this chapter because the goal was to examine edge and area effects on native plant communities in forest fragments.

5.2.3 Selection of edge gradients

See **Chapter 2, section 2.2.3** for a full description of the methods used to select the edge gradient sampled at each forest fragment. Note that only edge distances inside forest fragments were used in this chapter (-0.33, -4, -8, -16, -32, -64 and -128 m from the edge) because the focus of this study was on native plant communities inside forest fragments (see **Table 2.1** for the length of edge gradient sampled at each fragment).

5.2.4 Vegetation surveys

Vegetation at the study sites was surveyed from December 2004 to May 2005, November 2005 to May 2006, and January 2007. The percent foliage cover of native and exotic vascular plant species in each plot was estimated in three height tiers: ground (<0.5 m), shrub (0.5 – 2.0 m), canopy (>2.0 m). Species not able to be identified in the field were collected, and specimens were later identified using taxonomic keys (Allan 1961; Healy & Edgar 1980; Webb *et al.* 1988; Edgar *et al.* 2000) or sent to Landcare Research Plant Identification Service (Lincoln, Canterbury, New Zealand). Percent cover data were converted to cover scores using the formula (David Norton, pers. comm.):

$$\text{Cover score} = \sum \%\text{cover} \times \log_{10}(\text{tier depth})$$

Plant traits

Species were categorized according to their life form and dispersal mechanism, as these life history traits are likely to influence plant responses to forest fragmentation (Jacquemyn *et al.* 2003; Kolb & Diekmann 2005). Traits were assigned to each species using information from the literature (Allan 1961; Moore & Edgar 1976; Poole & Adams 1994) and the Landcare Research Ecotraits online database (LandcareResearch Research 2007). Data on other life history traits (e.g. seed mass, seed longevity, flowering period) were not readily available for all of the native plant species in this study. Species were categorized into nine different life forms: herbaceous dicotyledons ('dicot herbs'), forest interior ferns ('interior ferns'), open-habitat ferns ('open ferns'), lianes, orchids, rushes/sedges, shrubs, and trees. Interior ferns comprised ferns and fern allies from the Aspleniaceae, Blechnaceae, Dennstaediaceae, Dryopteridaceae, Grammitidaceae,

Hymenophyllaceae, Lycopodiaceae, Ophioglossaceae, Osmundaceae, Polypodiaceae, Psilotaceae, and Thelypteridaceae families. Open ferns comprised species which occur in both forest and open habitats, from the Gleicheniaceae, Pteridiaceae, Dryopteridaceae, Cyatheaceae and Dicksoniaceae families. Monocotyledons (monocots) comprised species from the Iridaceae, Liliaceae, and Poaceae families. Rushes and sedges (Cyperaceae and Juncaceae) were combined into one group for analysis. Six types of dispersal mechanism were recognised, consisting of two biotic dispersal mechanisms: animal (endozoochory) and attachment (exozoochory); and four abiotic dispersal mechanisms: ballistic, water (hydrochory), wind (anemochory), and unspecialised (no specific dispersal mechanism).

5.2.5 Environmental variables

In total, 47 environmental variables were used to analyse native plant responses to forest fragmentation (**Table 5.1**). These consisted of three treatment variables, 32 plot, fragment and landscape variables, and 12 potentially confounding variables.

Treatment variables

Fragment area was $\log_{10}$ transformed and distance to the forest edge was $\log_2$ transformed, as edge gradients were sampled on a $\log_2$ scale (Ewers & Didham 2006b). Interactions between edge and area effects are known to occur, therefore an interaction between the area and edge treatments was calculated by multiplying their values together (Ewers *et al.* 2007).

Fragment and plot variables

A shape index was calculated for each forest fragment using the equation from Patton (1975):

$$\text{Shape index} = P/(200(\pi * A)^{0.5})$$

where P is the perimeter (m) and A is the area (ha) of the fragment. Perfectly circular fragments have a shape index of 1, whereas more complex shapes will have correspondingly higher values.

Hemispherical photographs of canopy cover were used as a surrogate for light intensity, as this method is significantly faster than direct measurements of PAR or PPFD using light sensors, and is known to be highly correlated with them (Comeau *et al.* 1998; Engelbrecht & Herz 2001). Hemispherical photographs were taken in each plot using a Nikon Coolpix 5700 digital camera with a FC-E9 fisheye lens (183° angle of view). The camera was mounted approximately 1 m off

the ground with a tripod and aligned to magnetic north. Photographs were taken during cloudy conditions to minimize the effect of sun flecks and variability in the amount of sunlight between plots. The aperture was set at F/7.1 and shutter speed to 1/15 second in order to standardise the exposure. Canopy cover percentages were calculated from the hemispherical photographs using Gap Light Analyser version 2 software (Frazer *et al.* 1999).

Grazing by livestock can have major effects on plant communities in forest remnants (Yates *et al.* 2000; Dorrough *et al.* 2006) therefore grazing intensity was estimated in each plot on a scale ranging from zero (no evidence of grazing by livestock) to four (high density of livestock present). The level was estimated from the number of stock observed, visible damage to vegetation, hoof prints or pugging, and the density of faeces.

Soil samples were taken in each fragment at 16 m from the forest edge using a soil auger driven to a depth of 20 cm. Additional samples were taken at five other edge distances at one fragment per landscape (+2, -1, -4, -8, and -32 m from the edge). A minimum of six cores were taken at each position and bulked. Samples were air dried, then ground through a 2 mm sieve. Total carbon, phosphorus, nitrogen, organic matter content and pH were determined by Analytical Research Laboratories Ltd, Napier, New Zealand. Soil phosphorus was measured using Olsen's method (Olsen *et al.* 1954). Total nitrogen was analysed with a LECO analyser using the Dumas method (Petit *et al.* 2004), where soils are introduced into a combustion furnace and oxidised in a pure stream of oxygen. The subsequent gas stream is analysed for nitrogen dioxide by a thermal conductivity detection cell and the results expressed as total nitrogen. Total carbon was analysed by the combustion method using a LECO Analyser. Organic matter content was calculated from organic carbon using a standard mathematical conversion (Peverill *et al.* 1999). New Zealand Soil Bureau maps (Mew & Ross 1980) were used to estimate the soil drainage level in each plot, which ranged from poor (2 – Kumara, Maimai soils), imperfect-poor (3), imperfect (4 – Ahaura mottled phase, Carton Hill, Moana soils), good-imperfect (5), to good (6 – Ahaura, Hochstetter, Hokitika, Ikamatua soil types).

Study sites occupied five LENZ level 4 classes (Leathwick *et al.* 2003b): M1.1a, M2.1a, O3.1c, O3.1d and O1.4a, and these were included as five binary variables (see **Appendix 1** for a full description of the classes). Four macroclimatic variables from the underlying layers of LENZ – mean minimum temperature of the coldest month, mean winter solar radiation, October vapour pressure deficit and monthly water balance ratio – were also included because of their importance for the distribution of New Zealand tree species (Leathwick *et al.* 1998).

Table 5.1. Descriptions of the 47 environmental variables used in ordination and regression analyses. Source data: LCDB2 = Land Cover database version 2 (MfE 2004), LENZ = Land Environments of New Zealand (Leathwick *et al.* 2003b), Topomap = New Zealand Map Series 260, 1:50,000 scale (Land Information New Zealand, Wellington), Soil Bureau = NZ Soil Bureau Map (Mew & Ross 1980), DEM = New Zealand 25 m digital elevation model.

Code	Description	Units	Data source
Treatment variables			
LogArea	Log_{10} (fragment area + 1)	ha	LCDB2
Edgedist	Log_2 distance from edge	m	Field survey
AreaEdge	Area by edge distance interaction (LogArea x Edgedist)		Field survey
Fragment and plot attributes			
ShapeInd	Fragment shape index		LCDB2
Canopy	Percentage canopy cover	%	Field survey
Grazing	Grazing intensity (0=none, 1=low, 2=med, 3=high, 4=v.high)	0-4 scale	Field survey
SoilpH	Soil pH	0-14	Soil samples
SoilP	Soil olsen soluble phosphorus	P ug/mL	Soil samples
SoilOM	Soil organic matter	% w/w	Soil samples
SoilN	Soil total nitrogen	% w/w	Soil samples
SoilCN	Soil carbon/nitrogen ratio	(ratio)	Soil samples
Drainage	Drainage class (2 = poor, 4 = imperfect, 6 = good)	2-6 scale	Soil Bureau
Tmin	Mean minimum temperature of coldest month	°C	LENZ
Junes	Mean winter solar radiation	$MJ.m^{-2}$/day	LENZ
Vpd	October vapour pressure deficit	kPa	LENZ
R2pet	Monthly water balance ratio	(ratio)	LENZ
LENZ75	LENZ level 4 class = M1.1a	binary	LENZ
LENZ94	LENZ level 4 class = M2.1a	binary	LENZ
LENZ96	LENZ level 4 class = O3.1d	binary	LENZ
LENZ123	LENZ level 4 class = O1.4a	binary	LENZ
LENZ150	LENZ level 4 class = O3.1c	binary	LENZ
Landscape variables			
NND	Distance to nearest native forest (nearest neighbour distance)	m	LCDB2
NearBuil	Distance to nearest building	m	Topomap
NearRoad	Distance to nearest road/railway	m	Topomap
– calculated within 6 landscapes with radii of 256, 512, 1024, 2048, 4096, 8192 m			
Buil	Number of buildings per km^2	no./km^2	Topomap
Road	Length of roads & railways per km^2	m/km^2	Topomap
Confounding variables			
Landscape	native forest cover within 3 km radius landscape	%	LCDB2
Altitude	Altitude	m.a.s.l.	DEM
Aspect	Aspect	°	Field survey
Lat	N (from NZ grid ref)/1000 & reset to 2,2	1000 m	Topomap
Long	E (from NZ grid ref)/1000 & reset to 2,2	1000 m	Topomap
LatLong	LatLong (spatial autocorrelation variable)		Topomap
Lat2	Lat^2 (spatial autocorrelation variable)		Topomap
Long2	$Long^2$ (spatial autocorrelation variable)		Topomap
Lat2Long	Lat^2Long (spatial autocorrelation variable)		Topomap
Long2Lat	$Long^2Lat$ (spatial autocorrelation variable)		Topomap
Lat3	Lat^3 (spatial autocorrelation variable)		Topomap
Long3	$Long^3$ (spatial autocorrelation variable)		Topomap

Landscape variables

Several landscape variables were calculated for each plot using GIS analysis of the NZ Land Cover database (MfE 2004) and digitized layers of New Zealand topographic maps (New Zealand Map Series 260, 1:50,000. Land Information New Zealand, Wellington) (see **Table 5.1**). The degree of isolation of each fragment was measured by the nearest neighbour distance (NND), which was calculated as the distance from each plot to the edge of the nearest other native forest fragment using the Distance Matrix extension in ArcView GIS 3.2a (ESRI 1996). Distances to the nearest building and road or railway were calculated using the same tool. These variables were included because they are likely to be correlated with the degree of human modification and disturbance in the landscape. The number of buildings and length of roads and railways were calculated within circular landscapes with radii of 256, 512, 1024, 2048, 4096 and 8192 m centred on each survey plot (based on a $\log_2$ scale, as this scale was also used for edge distances and fragment size classes).

Confounding variables

The site selection procedure aimed to minimise variation between the fragments and edges sampled, however there was some variability among sites for several key variables. Altitude (determined from the New Zealand 25 m digital elevation model) and aspect were considered to be potentially confounding variables. The effect of spatial autocorrelation on community composition was assessed using linear, quadratic and cubic combinations of latitude and longitude co-ordinates from the New Zealand Map grid (NZMG). NZMG values were recoded and then truncated to the nearest 1000 m in order to avoid removing the fine-scale spatial autocorrelation within edge gradients, as described by Ewers *et al.* (2007). In **Chapter 2** of this thesis, I found significant landscape forest cover treatment effects on plant species composition, as well as significant landscape forest cover by fragment area by distance from edge effects. For the purposes of this chapter, the percentage of native forest cover in the landscape (within a 3 km radius) was treated as a covariable in the models, as here the focus was on area and edge effects on native plants within forest fragments.

5.2.6 Statistical analyses

Edge and area effects on native plant community composition – all tiers

Canonical correspondence analysis (CCA), a direct gradient (or constrained) analysis technique, was used to explore the relationship between native plant species composition and the measured environmental variables (ter Braak 1986). CCA extracts the dominant gradients in species composition with the constraint that they must be linear combinations of the independent variables. CCA was used instead of linear ordination methods such as RDA because the gradient lengths were relatively long (>4) (Hill & Gauch 1980; Lepš & Šmilauer 2003). CANOCO 4.02 software was used to carry out all the ordinations (ter Braak 1997-1999). Prior to the ordinations, the degree of inter-correlation between the environmental variables was determined with Pearson correlations using Statistica 7.1 (StatSoft 2006). Two of the landscape-level variables, Buil4096 and Buil8192 (i.e. the number of buildings within a 4096 m and 8192 m radius landscape), were highly inter-correlated ($n = 295$, $r = 0.88$, $p < 0.001$), therefore Buil8192 was not included in subsequent analyses.

A CCA was first carried out using cover scores (all height tiers combined) as the species data. Because of the large differences in the heights of each tier, cover scores differed greatly between species that predominantly occupied upper tiers versus those that predominantly occupied lower tiers, thus masking variation in the relative abundance of rare species in the lower tiers. Therefore, in order to obtain relative measures of variation in response to habitat fragmentation across species, it was necessary to mean-standardise the relative abundance values (i.e. subtract the overall mean cover score for each species from its cover score in individual plots). These mean-standardised values per plot were expressed in units of standard deviations from the species' mean cover score, by dividing the mean-standardised plot value by the overall standard deviation of all cover score values for that species. Thus, this analysis presents variation in the relative responses of species to fragmentation, but it does not represent variation in the absolute cover of any one species. Subsequent analyses of absolute percent cover were conducted separately within each individual tier (see below). In the all-tiers analysis, the goal was to determine whether relative species' responses to fragmentation differed among life forms or among dispersal mechanisms.

In a preliminary CCA of the all-tiers data, all 47 environmental variables were included and forward selection was used initially to determine whether any of the 12 potential confounding variables (Landscape, Aspect, Altitude and the nine spatial autocorrelation variables) explained a

significant amount of the variance in the plant species data. If so, then these significant variables were partialled out of subsequent ordination analyses as covariables. A partial CCA was then carried out and forward selection was repeated with the remaining 35 environmental variables. In the forward selection procedure, a Monte Carlo test (with 999 random permutations) was used to test whether each variable explained a significant amount of the variation in plant species composition, in addition to the variables already selected. A Bonferroni-corrected significance level of $p = 0.001$ ($p = 0.05/47$ environmental variables) was used in the forward selection, in order to minimise the chance of Type I error resulting from the large number of environmental variables being tested. Downweighting of 'rare' species and bi-plot scaling were selected.

The marginal and conditional eigenvalues for each environmental variable were used to assess the effect of each variable on species composition: the marginal effect is the independent effect of a variable (added first in the model) on the response variable, whereas the conditional effect is the additional effect of a variable after accounting for the effects of the other environmental variables. The relationships between the environmental variables and each pCCA axis were assessed using intra-set correlations, as these tend to be a more stable measure than the inter-set correlations (ter Braak 1987). The intra-set correlations were calculated by multiplying the inter-set correlations by the total species-environment correlation for each axis (Lepš & Šmilauer 2003). A Monte Carlo test with 999 random permutations was used to test the significance of the first canonical axis and the final set of predictor variables in the pCCA (using a Bonferonni corrected significance level of $p = 0.001$). Species scores from the all-tiers pCCA (which indicate the relative position of each species along the ordination axes) were used to compare the responses of different plant life forms and dispersal modes to area and edge gradients. Analysis of variance with Tukey's HSD multiple comparisons of means test was used to determine whether there were significant differences ($p < 0.05$) in the mean species scores among life forms and among dispersal mechanisms.

Edge and area effects on native plant community composition – separate tiers

Separate ordination analyses (CCAs) were then carried out for each of the three height tiers: ground (<0.5 m), shrub (0.5-2.0 m) and canopy (>2.0 m). A preliminary CCA was carried out for each tier to determine whether any of the 12 potential confounding variables explained a significant amount of variation in species composition in that tier (using a Monte Carlo test with 999 random permutations and a Bonferroni corrected p-value of 0.001). A partial CCA was then carried out and forward selection was repeated with the remaining 35 environmental variables and up to 12 covariables for each tier.

Edge and area effects on species richness of different life forms and dispersal mechanisms

The effects of the treatment variables on native plant species richness per plot (in all height tiers) were analysed using generalised linear models (GLMs) in R 2.4.1 (R Development Core Team, 2006). Species richness of different life forms and dispersal modes was analysed in separate GLMs, in order to determine how different trait groups responded to the treatment variables. Three potential confounding variables (Landscape, Altitude and Aspect) were entered ahead of the treatment variables in the GLMs, in order to partial out their effects on the response variables, and Type I sums of squares was used to assess the significance of the treatment effects. The distance from edge effect was determined after accounting for the effect of fragment area.

5.3 RESULTS

In total, 209 native vascular plant species from 63 families were recorded in the 44 forest fragments (see **Appendix 2** for a list of native species). Trees and interior ferns were the most diverse life forms, with over 40 species in each group, followed by herbaceous dicots and shrubs (**Table 5.2**). Wind and animal dispersal were the main dispersal mechanisms, with approximately 50% of the species being wind-dispersed, and 32% being dispersed by animals (**Table 5.2**). Almost all of the native species (206 species) were recorded in the ground tier, 174 species occurred in the shrub tier, and 95 in the canopy tier.

Table 5.2. Life history traits assigned to the 209 native plant species recorded in forest fragments and the number of species in each category.

Life history trait	Category	Number of species
Life form	Interior fern	48
	Tree	44
	Herbaceous dicotyledon	29
	Shrub	26
	Rush/sedge	21
	Orchid	16
	Open fern	9
	Liane	9
	Monocotyledon	7
Dispersal mechanism	Wind	95
	Animal	67
	Unspecialised	33
	Attachment	9
	Ballistic	3
	Water	2

5.3.1 Edge and area effects on native plant community composition – all tiers

In the pCCA of all height tiers (mean-standardised cover score data from all height tiers combined), 31 environmental variables and 12 covariables explained significant variation in native plant species composition. The pCCA results showed that the first canonical axis had a very high species-environment correlation (91%) and explained approximately 17% of the species-environment relation (see **Appendix 6**). The intra-set correlations for each axis revealed that the environmental variables most highly correlated with pCCA axis 1 were the three treatment variables – distance from the edge (Edgedist), fragment area (LogArea), and the area by edge distance interaction (AreaEdge) – and the soil carbon to nitrogen ratio (SoilCN) (**Table 5.3**). The second ordination axis was most strongly correlated with distance from the edge. Pearson correlations between the treatment variables and the other environmental variables indicated that fragment area was significantly correlated with several other variables; most strongly with fragment shape index, SoilCN, nearest neighbour distance, grazing intensity, and drainage level (see **Appendix 7**). The positive correlations with SoilCN ($r = 0.294$, $p < 0.001$) and drainage ($r = 0.173$, $p = 0.003$) indicate that soil nitrogen availability and drainage were higher in small fragments. Fragment area was negatively related to grazing intensity ($r = -0.190$, $p = 0.001$), meaning that grazing pressure was higher in small fragments. Distance from the edge was not correlated with any of the measured environmental variables, apart from percentage canopy cover, which increased significantly towards fragment interiors ($r = -0.316$, $p < 0.001$, **Appendix 7**).

The species scores from the pCCA (which indicate their relationship with each canonical axis) revealed that different groups of species within the native plant community responded differently to the major environmental gradients. Average axis 1 species scores differed significantly among life forms (ANOVA, $F_{8,200} = 5.486$, $p < 0.001$, **Figure 5.1a**) and dispersal mechanisms (ANOVA, $F_{5,203} = 3.388$, $p = 0.006$, **Figure 5.1b**). The average axis 1 score for herbaceous dicots was significantly higher than the average scores for orchids, shrubs, interior ferns (Tukey's HSD, $p < 0.001$), and monocots (Tukey's HSD, $p = 0.018$). Species with unspecialised dispersal had significantly higher average scores than wind- (Tukey's HSD, $p = 0.006$) and animal-dispersed species (Tukey's HSD, $p = 0.013$). Average axis 2 species scores differed significantly among life forms (ANOVA, $F_{8,200} = 2.00$, $p = 0.048$, **Figure 5.2a**), with the average score for rushes and sedges being significantly lower than the average score for trees (Tukey's HSD, $p = 0.04$). In contrast, there was no significant difference in average scores among species with different dispersal mechanisms (ANOVA, $F_{5,203} = 1.228$, $p = 0.297$, **Figure 5.2b**).

The main environmental gradients correlated with each axis mean that species with high average pCCA axis 1 scores tended to occur in smaller fragments and in plots with low C/N ratios (i.e. high nitrogen availability), whereas species with high pCCA axis 2 scores tended to be found towards the interior of forest fragments away from the edge. The average axis 1 species scores therefore indicate that herbaceous dicots tended to occur in small fragments, whereas orchids, monocots, shrubs, and interior ferns tended to occur in larger fragments. Similarly, species with water, ballistic and unspecialised dispersal mechanisms tended to be found in small fragments. The average axis 2 species scores revealed that rushes, sedges and other monocots occurred near edges, as did water-dispersed species. In contrast, orchids tended to occur in fragment interiors, as did species with ballistic and attachment dispersal mechanisms.

Table 5.3. Intra-set correlations between the environmental variables and the first three axes of a pCCA (partial canonical correspondence analysis) of native plant species composition in all height tiers. Only variables explaining significant variation ($p < 0.001$) in plant species composition are shown. The effects of 12 significant covariables were partialled out in the pCCA. Correlations in bold are significant (p-value of 0.001). Codes for environmental variables are given in **Table 5.1**. Treatment variables are shown in bold.

Variable	Axis 1	Axis 2	Axis 3
AreaEdge	**0.521**	**-0.329**	-0.061
Edgedist	**0.449**	**-0.518**	**0.207**
Road512	**0.295**	0.183	**0.272**
SoilpH	**0.287**	0.074	-0.120
Tmin	**0.281**	0.077	**-0.243**
Road256	**0.247**	0.145	0.136
Buil512	0.184	-0.004	**-0.200**
Drainage	0.182	0.066	0.030
SoilP	0.177	0.016	0.088
Buil256	0.126	-0.077	-0.094
NND	0.124	**0.257**	**0.301**
Grazing	0.119	-0.162	-0.172
JuneS	0.089	0.127	0.056
Buil1024	0.049	-0.011	-0.183
LENZ96	0.021	0.098	0.016
Road8192	0.009	**0.276**	0.099
Road2048	-0.035	**-0.238**	0.063
LENZ75	-0.044	-0.048	-0.017
Buil2048	-0.062	-0.180	-0.145
SoilN	-0.065	-0.071	0.051
Road4096	-0.076	-0.115	0.073
LENZ150	-0.085	0.048	**0.252**
SoilOM	-0.158	-0.064	0.161
NearRoad	-0.166	0.052	**-0.244**
R2pet	-0.183	0.000	**0.232**
Canopy	**-0.252**	**0.355**	-0.199
Buil4096	**-0.266**	**-0.248**	0.143
NearBuil	**-0.279**	0.004	0.197
ShapeInd	**-0.289**	-0.082	**0.367**
SoilCN	**-0.406**	-0.085	**0.369**
LogArea	**-0.412**	-0.049	**0.441**

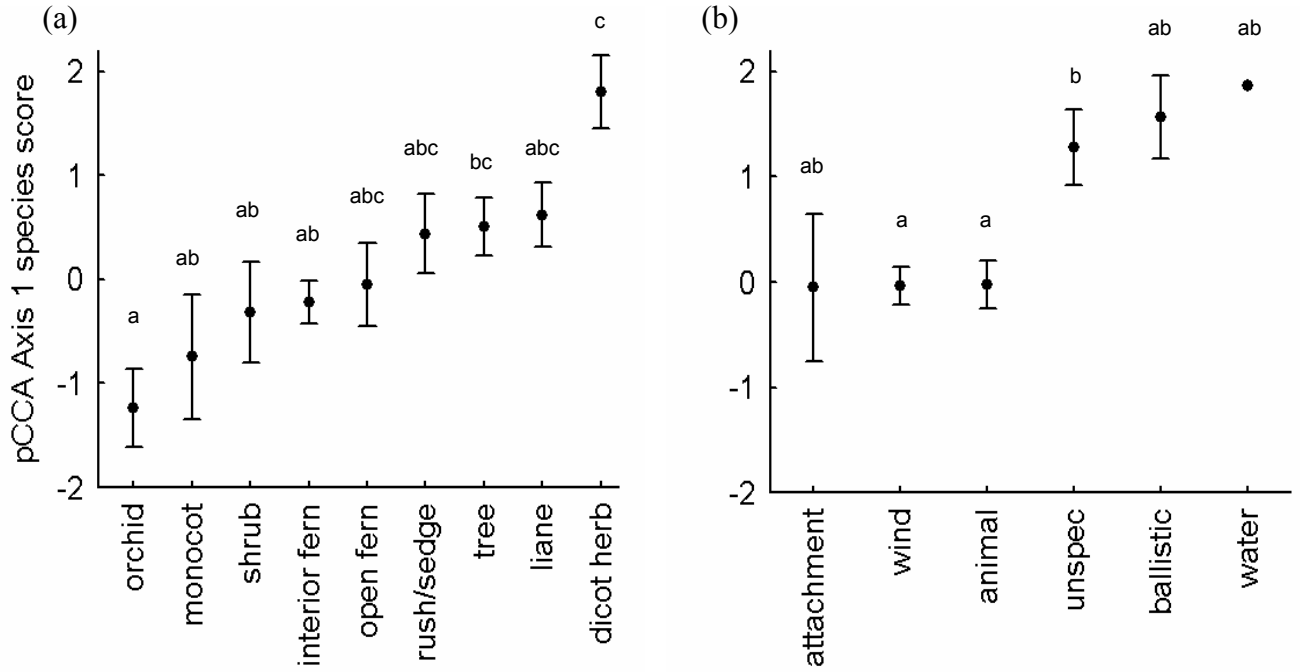


Figure 5.1. Mean axis 1 species scores per (a) life form and (b) dispersal mechanism from a partial canonical correspondence analysis (pCCA) of native plant species composition in all height tiers at 44 forest fragments. The effects of 12 significant covariables were partialled out in the pCCA. Error bars show standard error. Means with the same letters are not significantly different from each other (Tukey HSD test, $p < 0.05$). See Methods for a description of the trait categories.

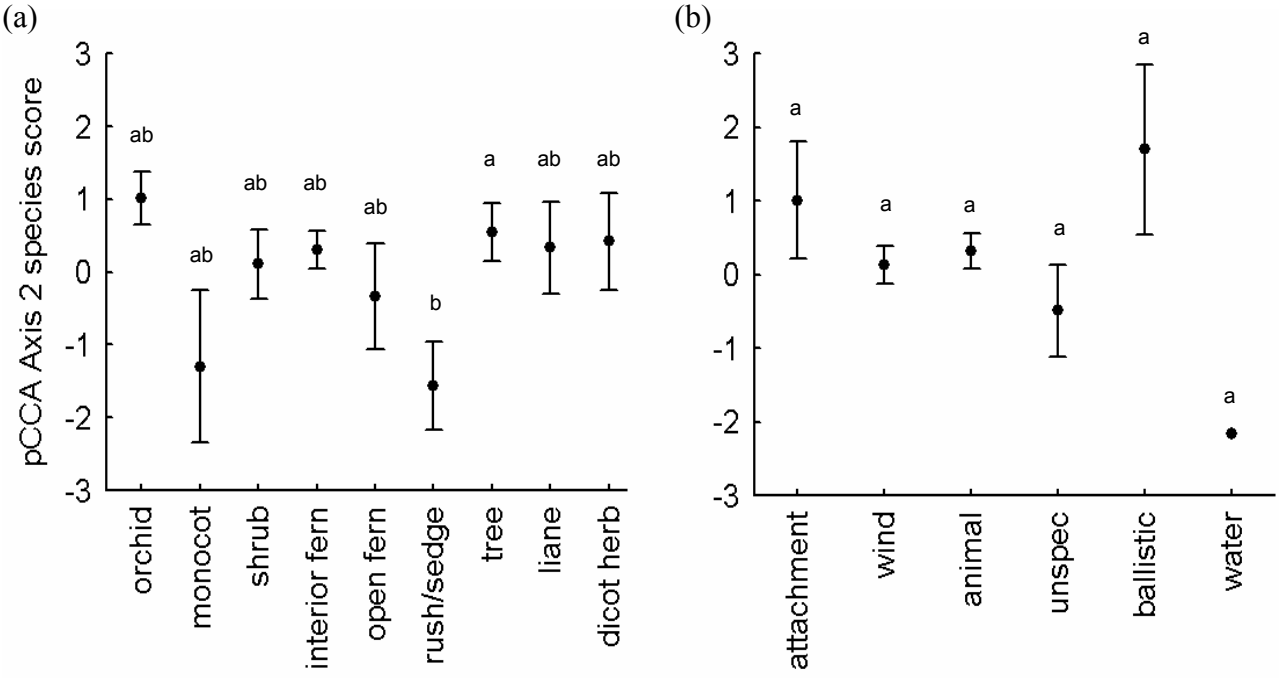


Figure 5.2. Mean axis 2 species scores per (a) life form and (b) dispersal mechanism from a partial canonical correspondence analysis (pCCA) of native plant species composition in all height tiers at 44 forest fragments. The effects of 12 significant covariables were partialled out in the pCCA. Error bars show standard error. Means with the same letters are not significantly different from each other (Tukey HSD test, $p < 0.05$). See Methods for a description of the trait categories.

5.3.2 Edge and area effects on native plant community composition – separate tiers

The separate ordinations of plant species composition in the different height tiers revealed that community composition in each tier was strongly related to the measured environmental variables (**Table 5.4**). However, the effects of the three treatment variables differed among the different tiers (**Table 5.5**).

Table 5.4. Results from partial canonical correspondence analyses (pCCA) of native plant community composition in three height tiers: Ground (<0.5 m), Shrub (0.5-2.0 m), and Canopy (>2.0 m). The sum of all unconstrained eigenvalues is after fitting the covariables. Percentages are taken with respect to residual variances i.e. variances after fitting the covariables. A Monte Carlo test with 999 random permutations was used to test the significance of the first canonical axis and all canonical axes in each pCCA.

		Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Ground tier (<0.5 m)						
Environmental variables	29					
Covariables	8					
Eigenvalues		0.358	0.277	0.232	0.187	7.940
Species-environment correlations		0.892	0.839	0.774	0.847	
Cumulative percentage variance						
of species data		5.3	9.3	12.8	15.5	
of species-environment relation		16.1	28.5	39.0	47.4	
Sum of all unconstrained eigenvalues						6.795
Sum of all canonical eigenvalues						2.224
		Significance of first canonical axis: F = 14.272, p <0.001				
		Significance of all canonical axes: F = 4.311, p <0.001				
Shrub tier (0.5-2 m)						
Environmental variables	18					
Covariables	12					
Eigenvalues		0.277	0.246	0.226	0.178	7.923
Species-environment correlations		0.848	0.794	0.796	0.723	
Cumulative percentage variance						
of species data		4.4	8.2	11.8	14.6	
of species-environment relation		18.0	34.0	48.6	60.2	
Sum of all unconstrained eigenvalues						6.372
Sum of all canonical eigenvalues						1.542
		Significance of first canonical axis, F = 12.019, p <0.001				
		Significance of all canonical axes, F = 4.683, p <0.001				
Canopy tier (>2 m)						
Environmental variables	27					
Covariables	4					
Eigenvalues		0.290	0.270	0.244	0.207	6.485
Species-environment correlations		0.815	0.814	0.810	0.773	
Cumulative percentage variance						
of species data		5.1	10.0	14.3	18.0	
of species-environment relation		15.3	29.5	42.4	53.3	
Sum of all unconstrained eigenvalues						5.622
Sum of all canonical eigenvalues						1.897
		Significance of first canonical axis, F = 14.334, p <0.001				
		Significance of all canonical axes, F = 5.170, p <0.001				

Distance from the edge (Edgedist) had a strong influence on native plant species composition in the two lower tiers, as shown by the large marginal and conditional eigenvalues for the ground and shrub tiers (**Table 5.5**), and significant intra-set correlations with the first three pCCA axes (**Table 5.6**). In contrast, species composition in the canopy tier was only weakly related to distance from the edge, and was more highly correlated with broader-scale soil and climate factors such as mean winter solar radiation (JuneS), soil C/N ratio, soil pH, and the land environment classes M2.1a, O1.4a, and O3.1c (LENZ94, LENZ123, and LENZ150). LENZ class M2.1a represents very gently undulating floodplains with recent, well-drained soils of high fertility, while classes O1.4a and O3.1c comprise gently undulating plains with well-drained and imperfectly-drained soils of moderate fertility (see **Appendix 1** for a description of the LENZ classes).

Fragment area explained significant variation in the species composition of all tiers (**Table 5.5**) and was highly correlated with the first pCCA axis for each tier (**Table 5.6**). The fragment area by distance from edge interaction was the most significant predictor of ground tier composition, and was highly correlated with ground tier pCCA axis 1, but appeared to be less important for the other tiers (**Tables 5.5** and **5.6**). This significant interaction effect is illustrated in **Figure 5.3**, where the slope of the edge gradient in ground tier composition increased with fragment area (**Figure 5.3a**), i.e. edge gradients in species composition tended to be steeper in larger fragments (see examples in **Figure 5.3b**).

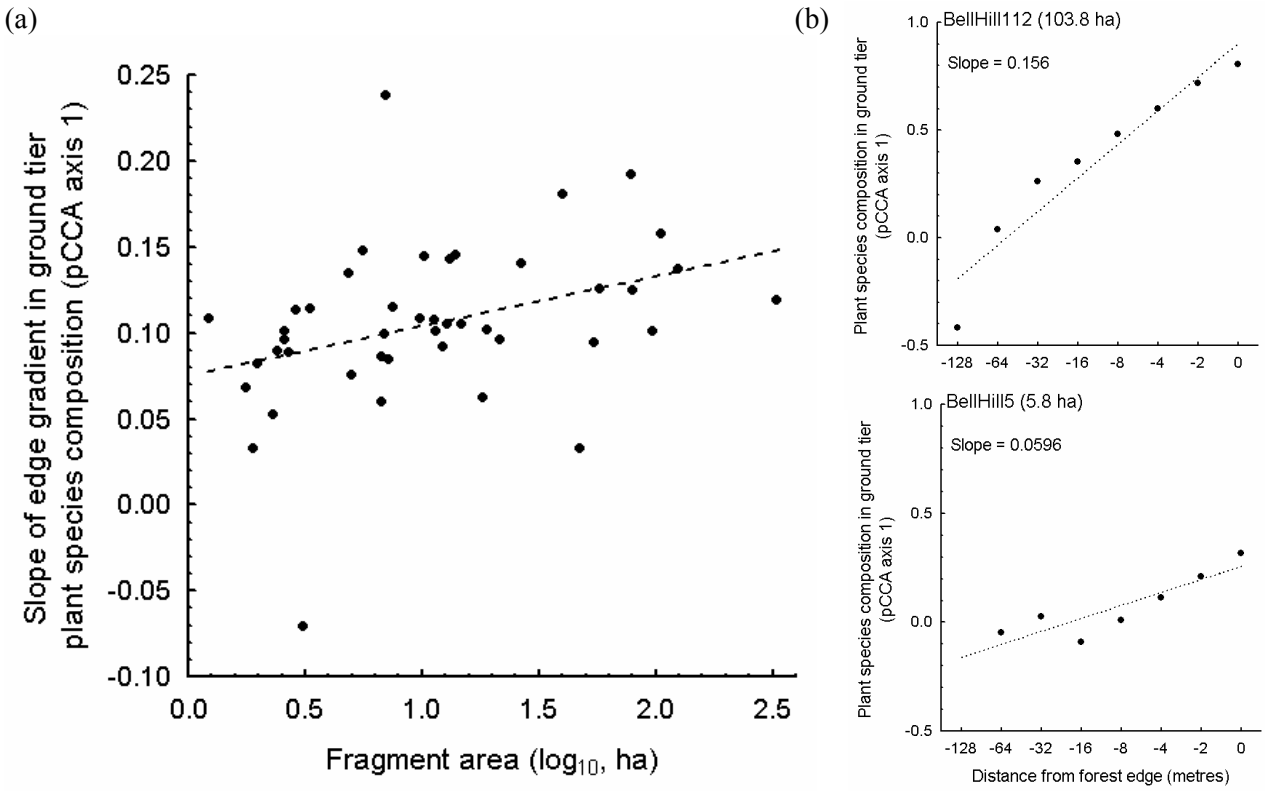


Figure 5.3. Fragment area and distance from the forest edge had a significant interaction effect on plant species composition in the ground tier: (a) the slope of the edge gradient in ground tier plant species composition increased with fragment area (n = 44). (b) The slope of the edge gradient at each fragment was calculated from a linear regression between axis 1 sample scores from a partial canonical correspondence analysis (pCCA) of plant species composition in the ground tier (<2 m in height) and distance from the forest edge. The slopes of the edge gradients at two fragments of different sizes (BellHill112 and BellHill5) are shown as examples. The effects of 8 significant covariables were partialled out in the pCCA. Linear regression lines are shown.

In addition to the treatment variables, a number of the environmental variables appeared to have an important influence on plant species composition (**Tables 5.5** and **5.6**). The land environment class M2.1a (LENZ94) had large marginal and conditional eigenvalues for all three tiers (**Table 5.5**) and high correlations with axis 1 of the ground and shrub tiers and axis 3 of the canopy tier (**Table 5.6**). LENZ class O1.4a (LENZ123) also explained significant variation in the species composition of all three tiers. Of the soil variables, the soil C/N ratio was the most significant predictor of plant species composition, with high eigenvalues and high intra-set correlations with the axes of all tiers. The densities of buildings and roads in the surrounding landscape (e.g. Buil4096, Buil2048, and Road512) were significantly related to plant species composition in the lower tiers, but these landscape-level variables were less important predictors of canopy composition. The ground and shrub tier plant communities were also significantly related to percentage canopy cover (a surrogate for light intensity) and the intensity of grazing by livestock, whereas canopy composition was unrelated to these variables (**Table 5.5**).

Table 5.5. Results of the forward selection procedure in pCCA (partial canonical correspondence analysis) to determine which environmental variables explain significant variation in native plant species composition in three height tiers: Ground (0.5-2.0 m), Shrub (0.5-2.0 m) and Canopy (>2.0 m). Marginal effects of all environmental variables and conditional effects of variables that account for significant variation are shown. The marginal effect is the independent effect of a variable (added first in the model) on the response variable, whereas the conditional effect is the additional effect of a variable after accounting for the effects of the other environmental variables. Monte Carlo permutation tests (999 random permutations) with a Bonferroni corrected p-value of 0.001 were used to determine significance. The effects of significant covariables (Landscape, Aspect, Altitude, and the spatial auto-correlation variables) were partialled out in each pCCA. λ = eigenvalue (fit) of each variable, λ_a = increase in eigenvalue (additional fit). Codes for environmental variables are given in **Table 5.1**. Treatment variables are shown in bold. Variables are ordered from most to least significant.

Ground tier (0.5-2 m)				**Shrub tier (0.5-2 m)**				**Canopy tier (>2 m)**			
Marginal effects		**Conditional effects**		**Marginal effects**		**Conditional effects**		**Marginal effects**		**Conditional effects**	
Variable	λ	**Variable**	λ_a	**Variable**	λ	**Variable**	λ_a	**Variable**	λ	**Variable**	λ_a
AreaEdge	0.20	**AreaEdge**	0.20	**Edgedist**	0.18	**Edgedist**	0.18	LENZ94	0.21	LENZ94	0.21
LENZ94	0.19	LENZ94	0.17	Canopy	0.17	LENZ94	0.14	JuneS	0.16	JuneS	0.16
Edgedist	0.19	SoilCN	0.13	**AreaEdge**	0.16	SoilCN	0.12	SoilCN	0.16	**LogArea**	0.13
Canopy	0.19	Buil256	0.12	LENZ94	0.15	Grazing	0.12	**LogArea**	0.13	LENZ123	0.12
Road512	0.16	Grazing	0.11	Road512	0.14	Road4096	0.09	LENZ150	0.13	NearRoad	0.09
SoilCN	0.14	Canopy	0.11	SoilCN	0.14	Road512	0.08	LENZ123	0.12	SoilpH	0.09
Grazing	0.14	Road4096	0.10	Buil4096	0.13	Buil512	0.08	NND	0.11	**Edgedist**	0.08
LogArea	0.14	Road512	0.10	**LogArea**	0.13	R2pet	0.08	ShapeInd	0.10	SoilCN	0.07
Buil4096	0.13	Tmin	0.09	Road4096	0.11	Canopy	0.08	Drainage	0.09	ShapeInd	0.06
LENZ123	0.13	ShapeInd	0.08	Grazing	0.11	**LogArea**	0.07	Road8192	0.09	Buil256	0.06
Buil256	0.13	Buil2048	0.07	ShapeInd	0.10	JuneS	0.07	R2pet	0.09	NND	0.06
NND	0.12	R2pet	0.07	LENZ123	0.10	Vpd	0.06	NearRoad	0.09	SoilP	0.06
Vpd	0.11	Vpd	0.07	Road256	0.10	NND	0.07	Tmin	0.09	Road2048	0.06
NearRoad	0.11	Road8192	0.06	Tmin	0.09	Buil2048	0.06	SoilpH	0.09	Road512	0.05
Road256	0.11	Buil1024	0.06	JuneS	0.09	Drainage	0.06	LENZ96	0.08	Road8192	0.06
Road4096	0.11	**Edgedist**	0.06	SoilpH	0.09	LENZ123	0.06	**AreaEdge**	0.08	LENZ150	0.05
Buil512	0.10	Buil4096	0.06	NearRoad	0.09	Road2048	0.07	Vpd	0.08	Road4096	0.05
Road8192	0.10	Drainage	0.06	LENZ96	0.08	Buil1024	0.06	Road512	0.07	Vpd	0.04
R2pet	0.10	NearRoad	0.05	Buil2048	0.08			**Edgedist**	0.07	Road256	0.04
Road2048	0.09	Road256	0.05	NND	0.08			SoilP	0.07	NearBuil	0.05
JuneS	0.09	LENZ150	0.05	Road2048	0.07			NearBuil	0.06	LENZ75	0.05
SoilpH	0.09	SoilP	0.04	Vpd	0.07			Road4096	0.06	Buil2048	0.04
Buil2048	0.09	NND	0.04	Buil256	0.07			Grazing	0.05	Buil4096	0.05
Drainage	0.08	Buil512	0.04	SoilOM	0.06			Buil512	0.05	Buil1024	0.05
Tmin	0.08	JuneS	0.04	SoilP	0.06			SoilOM	0.05	Drainage	0.05

ShapeInd	0.08	SoilpH	0.04	R2pet	0.06			Canopy	0.05	Grazing	0.04
LENZ96	0.07	Road2048	0.04	NearBuil	0.06			Buil256	0.05		
SoilP	0.07	LENZ123	0.05	Buil512	0.06			Road2048	0.04		
NearBuil	0.07	**LogArea**	0.04	Road8192	0.06			Road256	0.04		
LENZ75	0.06			LENZ150	0.05			Buil4096	0.04		
Buil1024	0.06			SoilN	0.05			Buil1024	0.04		
SoilOM	0.05			LENZ75	0.05			Buil2048	0.03		
LENZ150	0.04			Drainage	0.05			SoilN	0.03		
SoilN	0.04			Buil1024	0.04			LENZ75	0.02		
Road1024	0.02			Road1024	0.03			Road1024	0.01		

Table 5.6. Intra-set correlations between the environmental variables and the first three pCCA (partial canonical correspondence analysis) axes for each vegetation height tier: Ground (0.5-2.0 m), Shrub (0.5-2.0 m) and Canopy (>2.0 m). Only variables explaining significant variation ($p < 0.001$) in plant community composition in each tier are shown. The effects of significant covariables (Landscape, Aspect, Altitude, and spatial auto-correlation variables) were partialled out in each pCCA. Correlations in bold are significant ($p \leq 0.001$). Codes for environmental variables are given in **Table 5.1**. Treatment variables are shown in bold.

Ground tier (0.5-2 m)				**Shrub tier (0.5-2 m)**				**Canopy tier (>2 m)**			
Variable	**Axis 1**	**Axis 2**	**Axis 3**	**Variable**	**Axis 1**	**Axis 2**	**Axis 3**	**Variable**	**Axis 1**	**Axis 2**	**Axis 3**
LENZ94	**0.558**	**-0.201**	-0.035	LENZ94	**0.417**	**0.342**	-0.189	SoilCN	**0.494**	**-0.250**	**-0.201**
AreaEdge	**0.515**	**0.290**	**0.232**	**Edgedist**	**0.410**	**-0.361**	**-0.334**	**LogArea**	**0.365**	0.001	0.131
Edgedist	**0.419**	**0.231**	**0.412**	Grazing	**0.343**	-0.144	**0.294**	LENZ150	**0.354**	-0.123	**-0.284**
Road512	**0.406**	**-0.305**	0.109	NND	**0.270**	**0.208**	-0.186	NearBuil	**0.261**	0.005	-0.153
NND	**0.307**	**-0.244**	-0.052	Road4096	0.165	**-0.284**	0.166	Vpd	0.135	**0.248**	-0.115
JuneS	**0.255**	**-0.286**	-0.028	Drainage	0.134	0.061	-0.012	Buil256	0.127	-0.016	0.111
SoilpH	**0.244**	-0.169	-0.087	Buil1024	0.077	-0.094	0.169	NND	0.095	-0.183	**0.327**
SoilP	**0.228**	0.042	0.065	Road512	0.034	**0.305**	**-0.461**	ShapeInd	0.049	-0.028	**0.221**
Road256	**0.224**	**-0.317**	**0.209**	JuneS	-0.011	**0.316**	-0.144	NearRoad	0.045	0.083	**-0.282**
Drainage	0.154	-0.137	0.112	Buil512	-0.011	-0.111	0.104	LENZ75	0.016	-0.013	0.034
Grazing	0.140	**0.325**	**-0.215**	R2pet	-0.056	-0.031	0.012	Grazing	0.012	0.078	0.144
Tmin	0.095	-0.134	-0.099	LENZ123	-0.086	**-0.247**	**0.242**	Road2048	-0.003	0.066	-0.065
Road8192	0.066	**-0.355**	0.031	Road2048	-0.128	**-0.281**	0.089	**Edgedist**	-0.021	0.102	-0.143
R2pet	0.029	**-0.297**	0.082	Vpd	-0.182	-0.061	-0.010	Buil1024	-0.026	-0.090	0.063
LENZ150	-0.008	0.058	-0.013	SoilCN	**-0.223**	**-0.374**	-0.002	Drainage	-0.030	**0.226**	**0.252**
Road4096	-0.047	**0.331**	-0.108	Buil2048	**-0.239**	**-0.224**	0.168	Road512	-0.059	**-0.194**	0.187
Buil1024	-0.055	**0.229**	-0.068	Canopy	**-0.312**	**0.369**	**0.432**	LENZ96	-0.079	**-0.245**	0.119
Buil512	-0.113	0.137	0.034	**LogArea**	**-0.431**	**-0.227**	-0.138	Buil2048	-0.085	-0.037	-0.112
NearRoad	-0.114	**0.322**	**-0.280**					LENZ94	-0.090	0.122	**0.537**
Buil256	-0.115	**0.191**	-0.031					Road256	-0.092	-0.069	0.092
Vpd	-0.133	0.116	0.010					Buil4096	-0.109	-0.178	0.021
Road2048	-0.157	**0.244**	0.072					Road8192	-0.161	**-0.201**	0.178
SoilCN	**-0.200**	**0.365**	-0.078					SoilP	-0.165	-0.117	**0.254**
Buil2048	**-0.226**	**0.207**	0.086					Road4096	-0.177	**-0.203**	0.037
ShapeInd	**-0.230**	-0.020	0.050					LENZ123	-0.179	**0.201**	-0.159
Buil4096	**-0.269**	**0.287**	-0.018					SoilpH	**-0.325**	-0.037	0.119
Canopy	**-0.329**	**-0.364**	**-0.438**					JuneS	**-0.419**	**-0.327**	**0.235**
LENZ123	**-0.361**	0.155	-0.026								
LogArea	**-0.402**	**-0.220**	0.147								

5.3.3 Edge and area effects on species richness of different life forms and dispersal mechanisms

The GLMs revealed that fragment area and distance from the edge had significant effects on mean species richness per plot of several different life forms and dispersal mechanisms (**Table 5.7**). However, the fragment area by distance from edge interaction was not significant in any models. Fragment area had a significant negative effect on mean species richness per plot of herbaceous dicots (**Figure 5.4a**), interior ferns (**Figure 5.4b**), lianes (**Figure 5.4c**), open ferns (**Figure 5.4d**), and shrubs (**Figure 5.4e**); a positive effect on monocots (**Figure 5.4f**), and no detectable effect on orchids, rushes and sedges, or trees (**Table 5.7**). Changes in the abundance (i.e. mean cover score per plot from all height tiers) of individual species in relation to fragment area are shown in **Figure 5.4** as examples of typical responses by different life forms.

Table 5.7. The effects of fragment area and distance from the edge on the species richness per plot of different life forms and dispersal mechanisms, as determined by generalised linear models (GLMs) with Type I SS. The effects of three confounding variables (Landscape, Aspect and Altitude) were partialled out ahead of the treatment variables in the GLMs. The distance from edge effect was calculated after accounting for the effect of fragment area. The slope indicates whether the relationship was negative or positive. N = 295 in all GLMs. Significance level: p <0.001***, p <0.01**, p <0.05*, NS = non-significant (p >0.05). See Methods for a description of the trait categories.

Life history trait	Fragment area				Distance from the edge			
	df	F	P	Slope	df	F	P	Slope
Life form	1,288				1,288			
Herbaceous dicot		34.934	<0.001***	–		4.988	0.026*	+
Interior fern		9.709	0.002**	–		4.317	0.039*	–
Liane		5.393	0.021*	–		1.803	NS	
Monocotyledon		9.076	0.003**	+		11.181	<0.001***	–
Open fern		21.251	<0.001***	–		28.600	<0.001***	+
Orchid		0.439	NS			19.080	<0.001***	–
Rush/sedge		0.105	NS			3.018	NS	
Shrub		6.187	0.013*	–		1.485	NS	
Tree		0.641	NS			16.293	<0.001***	–
Dispersal mechanism	1,288				1,288			
Animal		2.647	NS			13.096	<0.001***	–
Attachment		0.702	NS			0.365	NS	
Wind		8.735	0.003**	–		7.927	0.005**	–
Unspecialised		13.102	<0.001***	–		9.033	0.003**	+

Fragment area had a significant negative effect on the mean number of species per plot with wind (**Figure 5.5a**) and unspecialised (**Figure 5.5b**) dispersal mechanisms, but the number of animal-dispersed species (endozoochory and exozoochory) did not appear to be related to fragment area (**Table 5.7**).

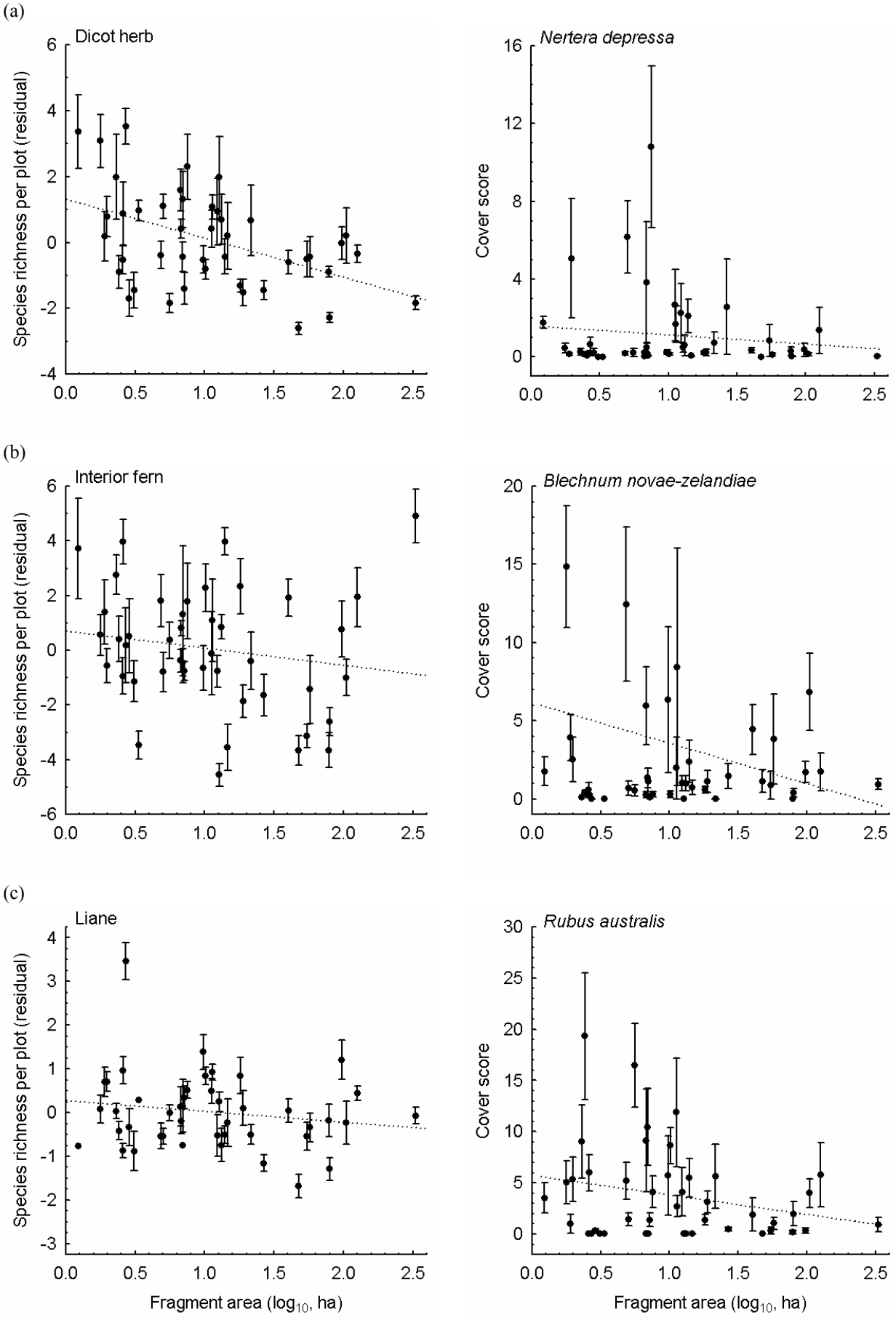


Figure 5.4 continued

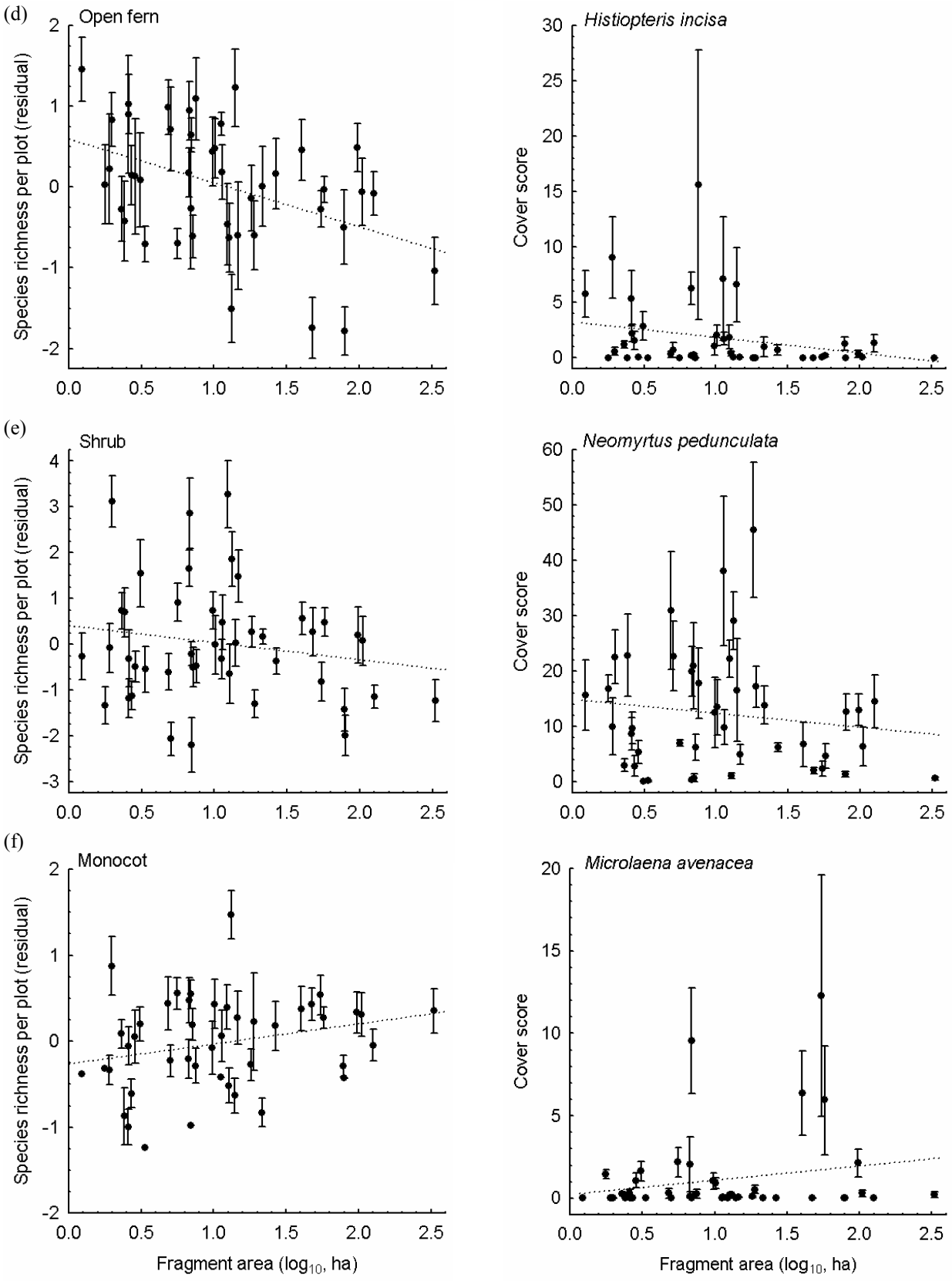


Figure 5.4. Mean species richness per plot of different life forms and mean cover score per plot (all height tiers) of representative species versus fragment area: (a) herbaceous dicot – *Nertera depressa*, (b) interior fern – *Blechnum novae-zelandiae*, (c) liane – *Rubus australis*, (d) open fern – *Histiopteris incisa*, (e) shrub – *Neomyrtus pedunculata*, and (f) monocot – *Microlaena avenacea*. See Methods for a description of the trait categories. Species richness per plot was calculated after partialling out the effects of 3 confounding variables (i.e. residual species richness). Error bars show standard error. Linear regression lines are shown.

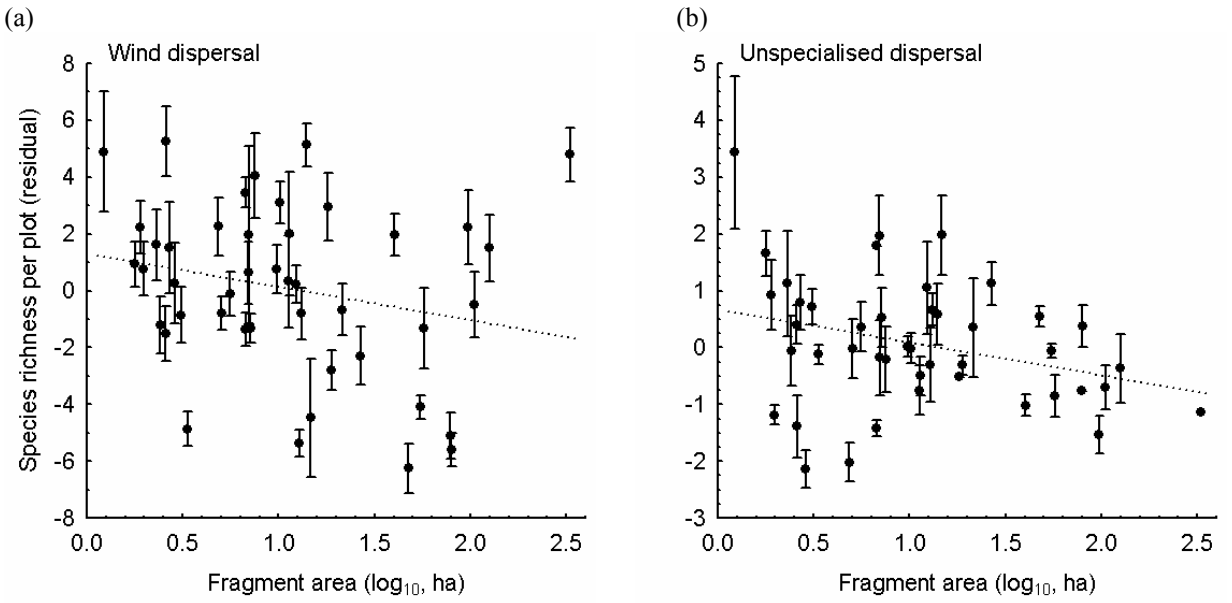


Figure 5.5. Mean species richness per plot of plants with different dispersal mechanisms versus fragment area: (a) wind and (b) unspecialised. See Methods for a description of the trait categories. Species richness per plot was calculated after partialling out the effects of three confounding variables (i.e. residual species richness). Error bars show standard error. Linear regression lines are shown.

Distance from the edge had a negative effect on mean species richness per plot of interior ferns (**Figure 5.6b**), orchids (**Figure 5.6d**), trees (**Figure 5.6e**), and monocots (**Figure 5.6f**) (i.e. species richness increased towards the interior of forest fragments), whereas species richness per plot of herbaceous dicots (**Figure 5.6a**) and open ferns was higher at edges (**Figure 5.6c**). Changes in the abundance (i.e. mean cover score per plot from all height tiers) of individual species in relation to distance from the forest edge are shown in **Figure 5.6** as examples of typical responses by different life forms. Distance from the edge had a negative effect on mean species richness per plot of animal- (**Figure 5.7a**) and wind-dispersed (**Figure 5.7b**) species, whereas the number of species with unspecialised dispersal was higher at edges (**Figure 5.7c**). Ballistic and water dispersal mechanisms were not able to be analysed with GLMs, as there were not enough species in these categories (see **Table 5.2**).

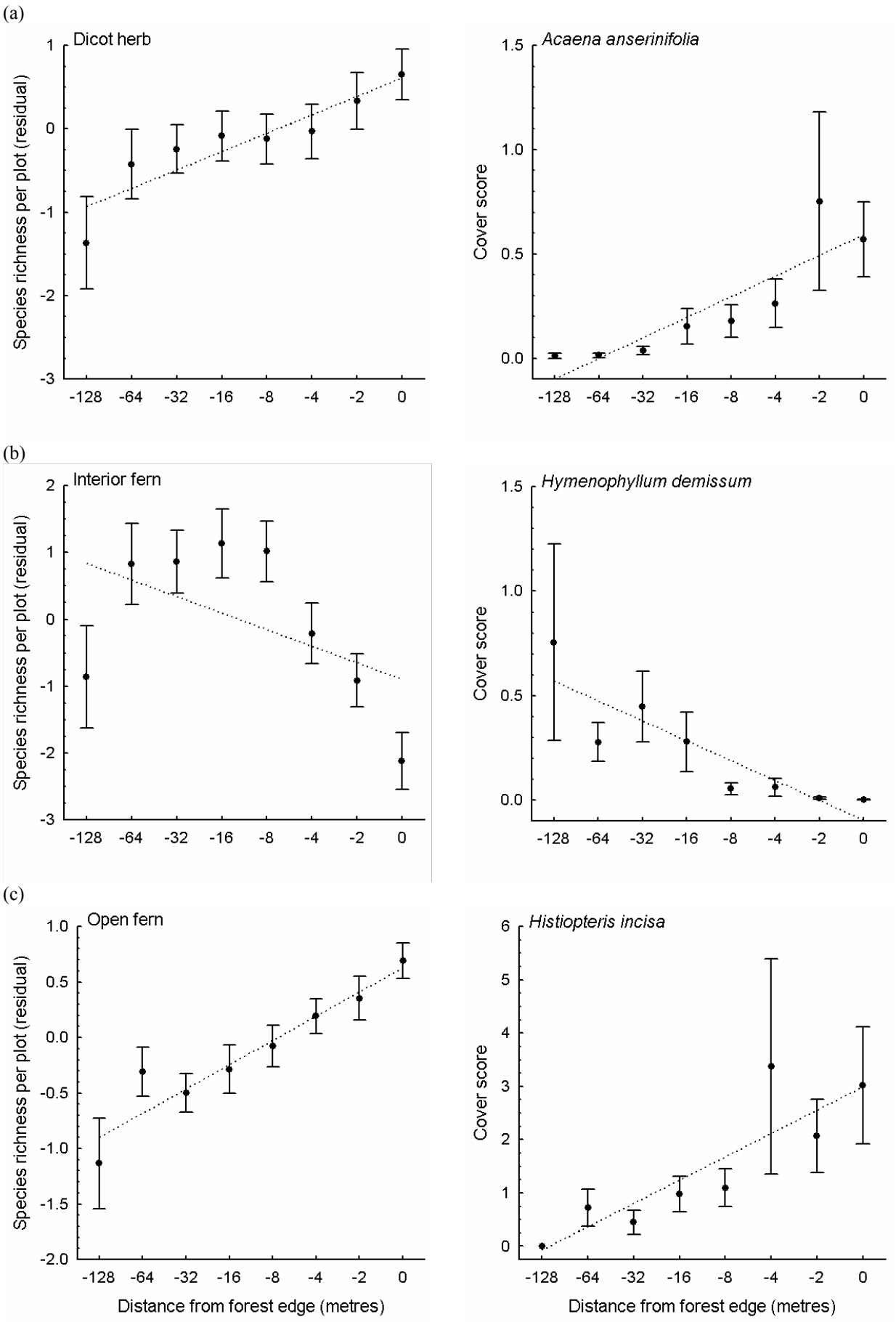


Figure 5.6 continued

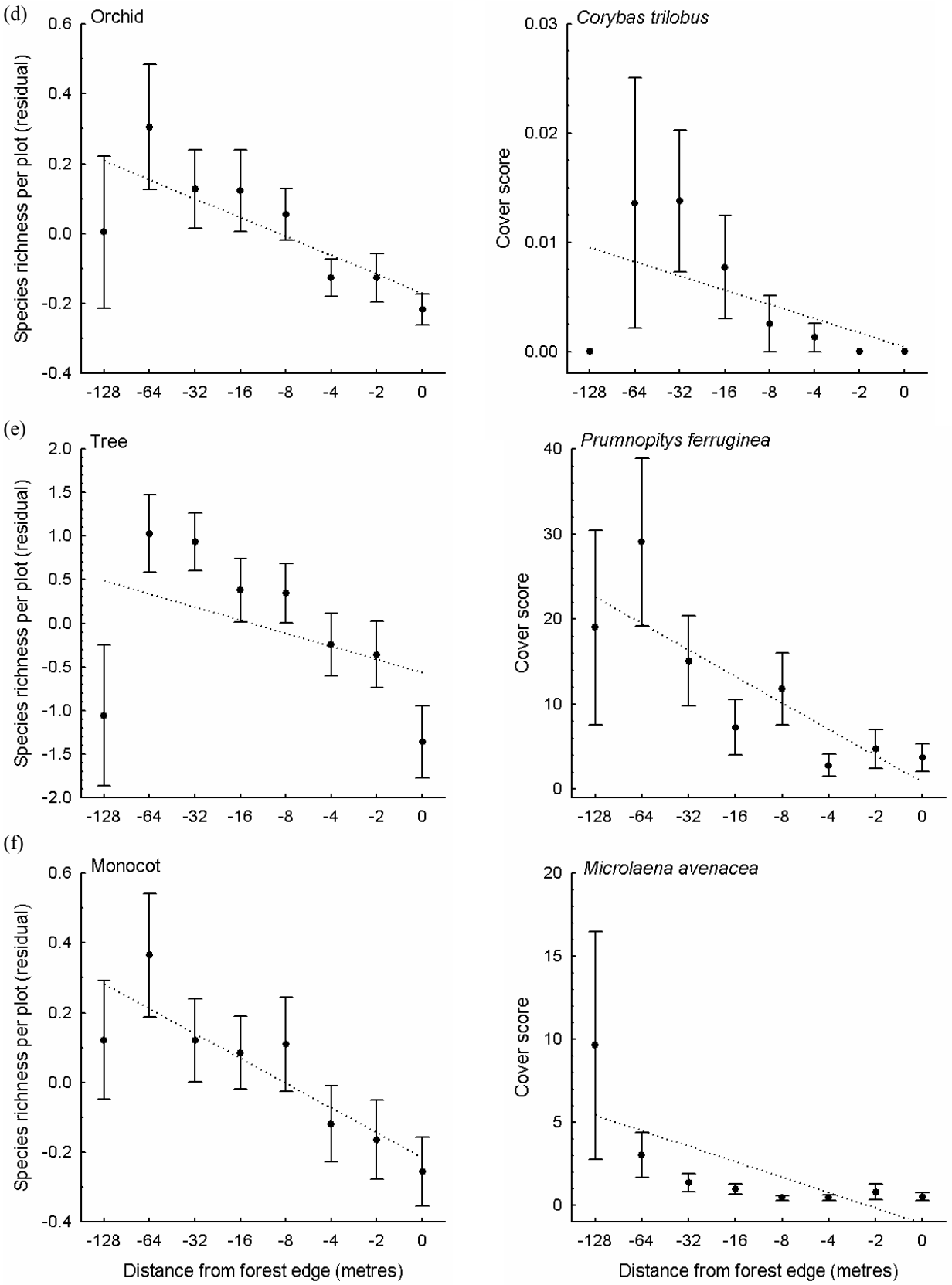


Figure 5.6. Mean species richness per plot of different life forms and mean cover score per plot (all height tiers) of representative species versus distance from the forest edge: (a) herbaceous dicot – *Acaena anserinifolia*, (b) interior fern – *Hymenophyllum demissum*, (c) open fern – *Histiopteris incisa*, (d) orchid – *Corybas trilobus*, (e) tree – *Prumnopitys ferruginea*, and (f) monocot – *Microlaena avenacea*. See Methods for a description of the trait categories. Species richness per plot was calculated after partialling out the effects of three confounding variables (i.e. residual species richness). Error bars show standard error. Linear regression lines are shown.

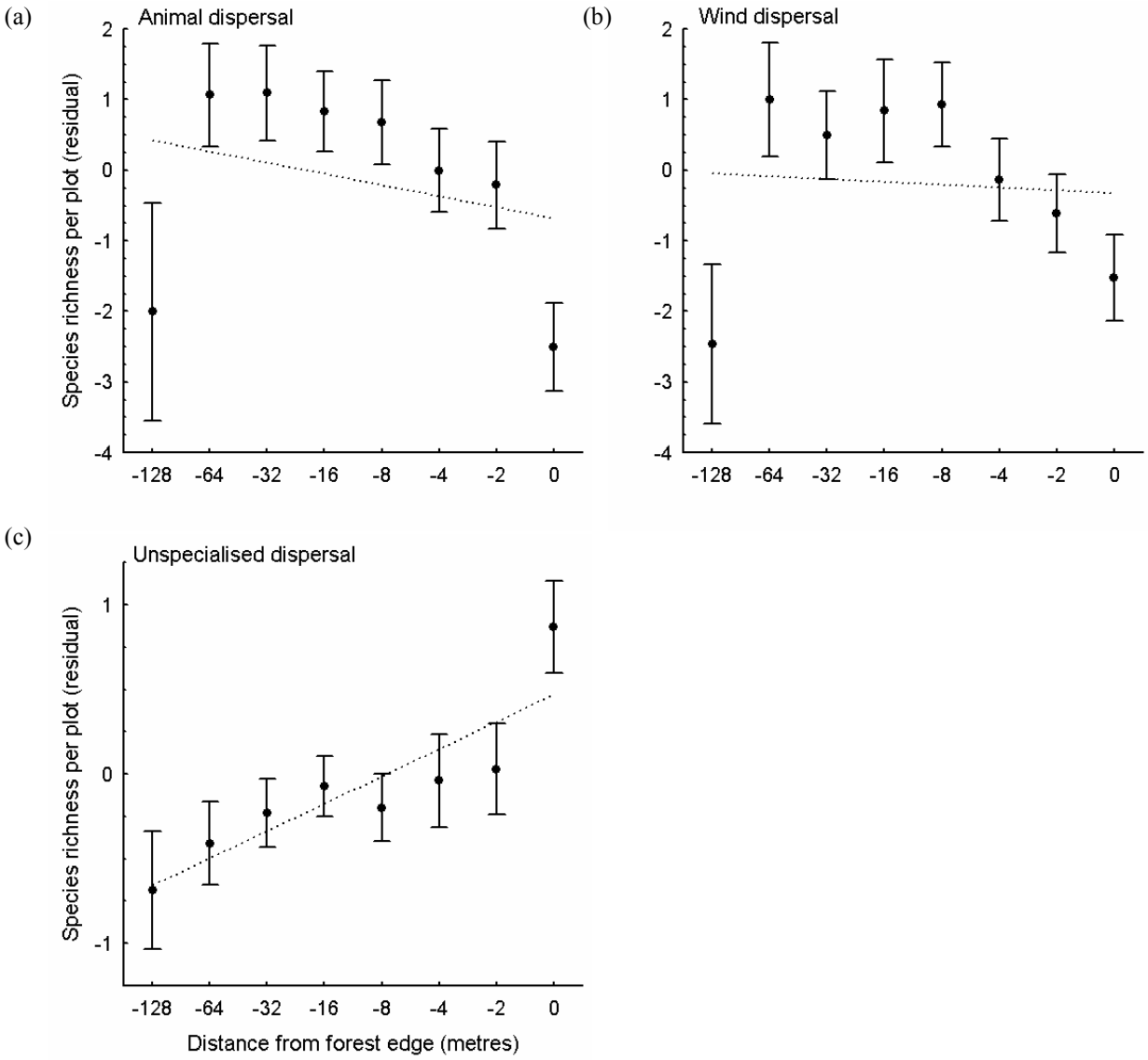


Figure 5.7. Mean species richness per plot of plants with different dispersal mechanisms versus distance from the forest edge: (a) animal, (b) wind, and (c) unspecialised. See Methods for a description of the trait categories. Species richness per plot was calculated after partialling out the effects of three confounding variables and fragment area (i.e. residual species richness). The x-axis is on a $\log_2$ scale. Error bars show standard error. Linear regression lines are shown.

5.4 DISCUSSION

5.4.1 Edge effects on native plant communities in forest fragments

Edge effects were found to vary spatially within plant communities, with species in the ground and shrub tiers exhibiting strong responses to the forest edge, whereas canopy composition was only weakly related to the edge gradient, and was more strongly related to broader-scale landform, soil and climate factors. Surprisingly few studies have examined the effects of fragmentation on the species composition of different forest strata, however one such study in Michigan, USA found that the penetration of edge effects was greater in the understorey than the canopy, with altered plant species composition being detected up to 45 m in the understorey, but only 20 m in the forest canopy (Palik & Murphy 1990). A range of other biotic responses (e.g. foliage density, growth rates, mortality) have also been shown to vary spatially within Amazonian forest fragments (Laurance *et al.* 2002).

As expected, species richness per plot increased towards the forest interior for most trait groups, confirming that the majority of native plant species in my study area may be considered to be forest interior specialists. These species are adapted to the low light and high humidity environments normally present in intact forests (Dawson 1993), and are therefore likely to be highly sensitive to edge effects. Although edge effects appeared to be detrimental to most native species in forest fragments, some groups of native plants appeared to respond positively to edge creation, as they were most diverse at edges – namely herbaceous dicots, open-habitat ferns, and species with unspecialised dispersal mechanisms. Herbaceous dicots and generalist ferns are commonly found in non-forest habitats in my study area, and the edge trends suggest that they have been able to take advantage of altered conditions at forest edges such as higher light intensity and air temperature. Similarly, a study in southern Chile found that forest fragmentation resulted in higher densities of shade-intolerant species and edge specialists in forest fragments (Echeverría *et al.* 2007). A previous study on the West Coast of New Zealand found increased densities of tree ferns and shrubs at north-facing edges of native forest fragments, however they did not present any data for species richness, so I cannot directly compare their results with my study (Norton 2002). The increase in species with unspecialised dispersal mechanisms at edges is more difficult to explain, but suggests that this strategy may be more common in open habitats. A previous study in Belgian forest fragments also found that the abundance of species with no specific dispersal mechanism declined towards the forest interior (Devlaeminck *et al.* 2005).

Distance from the forest edge had no apparent effect on the species richness per plot of shrubs, rushes and sedges, or lianes, implying that these life forms have fairly general habitat requirements, and are able to occupy both forested and open habitats. Rushes and sedges are usually restricted to wet, open habitats, as they require relatively high soil moisture levels. However, the West Coast region receives very high rainfall (>2500 mm p.a.) and most soils have poor drainage (Leathwick *et al.* 2003b), so many forest fragments have high soil moisture levels year-round, and appear to provide suitable habitat for rushes and sedges. The number of shrub species did not change along the edge gradient, implying that shrubs were relatively unaffected by edge creation. However, the shrub group contained a wide range of species (26 in total) which are likely to have varying habitat preferences (Merrett *et al.* 2007), hence there may have been considerable species turnover of shrubs along the edge gradient, even though shrub richness did not change. Some studies have found that the density and diversity of lianes increased near edges following forest fragmentation (Laurance *et al.* 2001; Zhu *et al.* 2004), however there was no evidence for this in my study.

5.4.2 Area effects on native plant communities in forest fragments

Fragment area was an important predictor of plant species composition in all height tiers, and had significant effects on species richness per plot of 8 out of the 13 trait groups examined. Herbaceous dicots had the most significant relationship with fragment area, supporting my prediction that species with short life spans and faster generation times would display the strongest response to fragment area. Fragment area had a negative effect on species richness per plot of most trait groups; only monocot richness increased significantly with fragment area. The negative relationship between fragment area and species richness per plot was surprising, since smaller fragments are usually expected to support fewer species than large fragments (Burkey 1995). The response variables were calculated as species richness per plot rather than total species richness per fragment, however, therefore total species richness may have been higher in large fragments if entire fragments had been surveyed. It appears that the higher species richness per plot observed in smaller fragments may be driven by the underlying soil properties, as more fertile soils are expected to support higher species diversity (Chesson 2000), and soil nitrogen and drainage levels were higher in small fragments.

In contrast to most other trait groups, monocots had higher species richness per plot in larger fragments, suggesting that they have not benefited from the higher soil fertility levels in smaller fragments, and prefer to occupy forest interior habitats, which occur mostly in larger fragments.

The monocot group comprised four species from the Liliaceae family, one iris, and two grass species. Most of these species have relatively slow growth-rates and long life spans – characteristics which are common for forest-interior specialists (Craine *et al.* 2006).

Fragment area had no effect on the number of animal-dispersed species per plot, however the number of species with wind and unspecialised dispersal mechanisms decreased with fragment area. Similarly, a study in the montane rainforests of southeastern Brazil found a negative relationship between fragment size and the relative importance of tree and shrub species with abiotic dispersal mechanisms (Tabarelli *et al.* 1999). My results also imply that species with abiotic dispersal mechanisms may have higher rates of seed dispersal in fragmented landscapes than species which depend on animals for dispersal. Few fragmentation studies have directly measured seed dispersal rates, but one such study in Michigan, USA revealed that wind-dispersed species had higher rates of seed dispersal than animal-dispersed species (McEuen & Curran 2004). Wind-dispersal is likely to be an advantage in fragmented landscapes, as wind speeds are usually higher (Laurance & Curran 2008), and this would assist long-distance dispersal between fragments. In contrast, populations of avian pollinators and dispersers may be reduced in fragmented landscapes, leading to a breakdown in plant-animal mutualisms (van Ruremonde & Kalkhoven 1991; Cordeiro & Howe 2001; Lennartsson 2002).

A number of the environmental variables measured in my study appeared to be important drivers of plant community composition in forest fragments. Soil fertility appeared to have a particularly strong effect, as the availability of nitrogen in the soil (as measured by the C/N ratio) was an important predictor of species composition in all vegetation tiers. The soil C/N ratio was highly correlated with fragment area, suggesting that the area effect on species composition may be partly explained by higher soil nitrogen availability in smaller fragments. Nitrogen levels may be higher in small fragments because they are subject to nutrient enrichment from fertiliser use on farmland in the surrounding landscape (Stevenson 2004). Another possibility is that these fragments had naturally higher soil fertility prior to fragmentation, as forest loss is usually greatest on the most productive soils (Lindenmayer & Luck 2005). Grazing intensity was higher in small fragments, and had a strong effect on understorey species composition, implying that grazing could act synergistically with the effects of reduced fragment area to modify species composition in forest fragments (Hobbs 2001; Laurance & Cochrane 2001). Grazing had much weaker effects on native species composition in the canopy and shrub tiers. This reflects the fact that grazing animals only have access to vegetation on the ground, and also implies that changes in ground species composition as a result of differential grazing pressure have occurred relatively recently,

and have not yet led to changes in the composition of the upper (older) height tiers among fragments.

5.4.3 Interactions between edge and area effects on native plant communities

Fragment area had a significant influence on the strength of edge effects on the ground tier community (as indicated by the significant area by edge distance interaction), with steeper edge gradients in species composition occurring in larger fragments. Similarly, a recent study in New Zealand reported synergistic interactions between edge and area effects on beetle communities in forest fragments, and found that edge gradients in beetle species composition were steeper in larger fragments (Ewers *et al.* 2007). The most likely explanation for the weak edge effects observed in small fragments is that they are influenced by the surrounding matrix more than large fragments, and therefore lack forest-like conditions because matrix conditions penetrate further into the fragment (Laurance & Yensen 1991; Malcolm 1994; Ewers *et al.* 2007). This results in the plant community inside small fragments being relatively similar to the community at the edge. In contrast, large fragments contain more forest interior habitat, resulting in a greater change in species composition along the edge gradient. As Ewers *et al.* (2007) noted, this interaction effect has important implications for the conservation of native communities in fragmented landscapes because the rates of loss of edge-intolerant species from small fragments will be higher than expected from fragment area alone. Surprisingly, the area by edge interaction did not have any significant effects on native species richness per plot in my study, emphasising the need to consider species composition as well as richness when investigating the effects of fragmentation on forest communities (Aparicio *et al.* 2008).

Chapter 6 – Conclusions and future directions for research on invasions in fragmented landscapes

The previous chapters of this thesis have explored different aspects of the effects of habitat fragmentation and invasions on plant communities in native forest fragments. In this chapter, I will briefly summarise the conclusions from these five chapters, suggest future directions for research on fragmentation and invasions, and discuss some of the implications from my study for the conservation of native plant species in fragmented landscapes.

6.1 CONCLUSIONS FROM MY RESEARCH

6.1.1 The interacting effects of fragmentation on plant invasions

My study constitutes the first empirical investigation of the multiple interactions between edge, area, and landscape effects on plant communities in forest fragments, and is the first study to examine the influence of these factors on invasion processes in fragmented landscapes. My research has revealed that plant communities in forest fragments are influenced by the effects of fragmentation and landscape modification at a range of spatial scales, and suggests that synergistic interactions between these factors may have promoted invasions by exotic plants. The degree of exotic dominance in the plant community was highest at forest edges and decreased towards fragment interiors, however the interiors of very small fragments were relatively more invaded by exotic plants than those in larger fragments, reflecting a significant interaction between edge and area effects. The effects of landscape cover on plant communities were more complex, as landscape cover appears to interact strongly with edge and area effects (in a three-way interaction), and with other landscape-scale factors. My research revealed that the amount of forest cover in the landscape appeared to influence the strength of edge and area effects on the plant community, as the degree of edge-mediated invasion increased as forest cover in the landscape decreased, but this effect was only apparent in very small fragments (<2 ha). My results suggest that the combined effects of small fragment size and low forest cover in the landscape may have promoted invasions by exotic plants in these fragments.

6.1.2 Mechanisms underlying plant invasions in fragmented landscapes

My study sought to understand the mechanisms underlying invasions of exotic plants in fragmented landscapes, and to tease apart some of the inter-correlated factors affecting different stages of the plant invasion process. In particular, I wanted to explore whether propagule availability and/or habitat suitability were limiting invasions of exotic plants in native forest fragments, and whether fragmentation has led to higher invasibility of forest fragments to exotic plants. Experimental addition of exotic plant propagules suggested that habitat suitability limited the invasions of some exotic species, as there were significant landscape forest cover by distance from edge interaction effects on the germination, growth, and/or flowering responses of two short-lived, herbaceous species (*Digitalis purpurea* and *Prunella vulgaris*). The significant interaction effect reflects the fact that these species established and grew better at fragment edges in landscapes with a low proportion of native forest cover. Analysis of a number of environmental covariates revealed that light intensity and soil phosphorus levels were higher at fragment edges in low forest cover landscapes, suggesting that these factors may have been driving some of the landscape cover by distance from edge interaction effects on *D. purpurea* and *P. vulgaris* responses. Heavily deforested landscapes usually have a higher intensity of human land use and modification, and this will lead to higher levels of disturbance (e.g. reduced canopy cover and nutrient enrichment) in forest fragments in these landscapes (McIntyre & Hobbs 1999; Fischer & Lindenmayer 2007). These disturbances are likely to increase the invasibility of forest fragments, as some exotic plant species may be able to exploit these altered conditions better than native species (Allcock 2002; King & Buckney 2002; Howard *et al.* 2004; Leishman & Thomson 2005).

6.1.3 The influence of traits on plant responses to fragmentation

My research revealed that fragmentation has a variety of effects on plant communities in forest fragments, and highlighted the importance of examining species traits in order to understand the responses of plant species to forest fragmentation. Firstly, I examined whether certain traits influenced the invasiveness of exotic plants in different habitats. My results revealed that a combination of life history traits, and the history and distribution of the species in New Zealand determined their invasiveness in forest fragments. Traits associated with invasiveness at fragment edges were being a perennial, monocot, shrub or fern, having low shade tolerance and wind dispersal, and being introduced early to New Zealand, for agricultural or horticultural purposes. In contrast, traits associated with invasiveness in fragment interiors were being a fern or shrub, having high shade tolerance, wind dispersal, and being introduced for ornamental reasons.

Native plant species also differed in their responses to forest fragmentation, with some groups of species responding negatively to edge effects, while others appeared to respond positively. Species richness per plot of interior ferns, monocots, orchids, and trees, and plants with animal and wind dispersal mechanisms increased towards the fragment interior. In contrast, the number of species per plot increased towards the edge for herbaceous dicots and open-habitat ferns. The results support the findings of previous studies (Grashof-Bokdam 1997; Bender *et al.* 1998; Gascon *et al.* 1999) which have suggested that generalist species that can occupy both forest and open habitats (e.g. herbaceous dicots and some ferns in my study) may have benefited from forest fragmentation because they are able to utilise edge habitats, whereas forest specialists (e.g. most native trees, ferns, monocots in my study) are more likely to be negatively impacted by forest fragmentation. The influence of dispersal mechanism on species responses to fragmentation was more variable, however my results suggested that abiotic dispersal mechanisms (e.g. wind, unspecialised dispersal) may be an advantage in the deforested landscapes of my study area.

6.2 FUTURE RESEARCH DIRECTIONS

6.2.1 The influence of the matrix on plant invasions in fragmented landscapes

Characteristics of the surrounding landscape will have a major influence on plant communities in forest fragments, and processes occurring in the matrix are likely to play a key role in driving invasions in fragmented landscapes (Davies *et al.* 2001; Hobbs 2001; Murphy & Lovett-Doust 2004; Kupfer *et al.* 2006). Human land use and management activities in the matrix are likely to enhance the establishment and spread of many exotic plants, therefore the matrix will act as the main reservoir of exotic plant propagules in fragmented landscapes and determine the level of exotic propagule pressure on fragments (With 2002). Human activities in the matrix will also influence the invasibility of forest remnants in fragmented landscapes. In general, the higher the degree of human modification of the landscape, the more susceptible to invasion the remaining fragments will be. Despite the obvious importance of the matrix in influencing invasion processes in fragmented landscapes, there has been relatively little research to quantify the level of disturbance in the matrix necessary to promote invasive spread (With 2002). It is possible that there could be a threshold in the level of human modification and disturbance in the matrix for invasive spread to occur (analogous to the 'extinction threshold hypothesis'). Once the matrix threshold is reached, the rate of invasion by exotic species could increase rapidly, and exacerbate the impacts of landscape modification on native species.

In my study, I focussed on the effects of the amount of native forest cover in the landscape on the dominance of exotic plants in forest fragments, however I also tried to assess the effects of human land use intensity in the matrix using correlates such as the density of buildings and roads in the landscape. Surprisingly, these measures of human disturbance in the landscape appeared to have relatively little effect on the dominance of exotic plants in forest fragments, even though the amount of forest cover had a significant effect. My study highlights the difficulty in quantifying the intensity of human activities in the surrounding landscape, and reinforces the need for better understanding of the role of human management activities in driving exotic plant invasions in fragmented landscapes.

6.2.2 The role of propagule pressure in driving invasions

A number of studies have emphasised the importance of propagule pressure in driving the invasion process (Stohlgren *et al.* 2001; Kowarik 2003; von Holle & Simberloff 2005; Drake & Lodge 2006; Richardson & Pysek 2006), however the difficulty in measuring propagule pressure, particularly at landscape scales, has hindered our ability to fully understand the mechanisms driving invasions, and to determine the importance of propagule pressure relative to other factors such as habitat invasibility (Stohlgren *et al.* 2001; Richardson & Pysek 2006). Further research is needed to understand how landscape modification affects the regional exotic species pool, and how interactions with humans may influence the abundance and spread of exotic species in fragmented landscapes. Further long-term experimental work involving the addition of seeds and seedlings of a range of exotic species, in conjunction with habitat manipulation, would also be beneficial for assessing the extent to which propagule pressure can overcome low habitat invasibility (Richardson & Pysek 2006).

6.2.3 The effect of landscape thresholds on invasive spread

Although the amount of forest cover in the landscape had a significant effect on the degree of exotic dominance in the plant community, there was no indication in my study that invasions by exotic plants into forest fragments had increased abruptly below a certain threshold of native forest cover in the landscape. It should be acknowledged, however, that my study landscapes contained ~20% or higher forest cover, therefore it is possible that these landscapes may currently be above the extinction threshold (Andrén 1994; Fahrig 2002). Detection of landscape thresholds also depends on whether the spatial scale of the landscape was appropriate for the system being studied (Huggett 2005; Lindenmayer & Luck 2005). My study examined the effects of landscape

context on the entire plant community, however different species within a community are likely to respond differently to spatial scale, hence it is difficult to select a landscape scale that is relevant for all species (de Blois *et al.* 2002). Because of these limitations in my study, further investigation using a range of landscape scales and a greater number of landscapes with less than 20% forest cover would be beneficial for determining the relevance of thresholds in landscape cover for invasions in fragmented landscapes.

6.3 IMPLICATIONS OF MY RESEARCH FOR CONSERVATION OF NATIVE SPECIES IN FRAGMENTED LANDSCAPES

6.3.1 The effects of forest fragmentation on native plant species

My research has increased our knowledge of the effects of habitat fragmentation on native plant species in lowland forest remnants, and revealed that the majority of native forest species are likely to be negatively affected by the creation of edges. The impacts of forest fragmentation were most apparent on understorey species, implying that edge effects may interact with other disturbances such as grazing to drive changes in species composition on the forest floor. High grazing intensity by stock, in combination with elevated light and temperature levels, is likely to lead to a shift in understorey plant species composition towards a more hardy, unpalatable native community with a higher degree of exotic dominance. A reduction in grazing pressure or complete exclusion of stock would clearly be beneficial for reducing the impacts of fragmentation on some sensitive native forest plants, particularly in very small forest fragments. The majority of native forest remnants in my study area were on private farmland, however, and were freely accessible to livestock. There was very little awareness among farmers of the value of lowland forest remnants for native plant species, and little concern about the negative impacts of stock on native remnants. It therefore seems likely that financial incentives would be necessary to encourage better management of forest remnants on private land.

Contrary to my predictions, larger fragments did not appear to support higher densities of native plant species than small fragments, however fragment area was strongly inter-correlated with other important drivers of plant species composition, such as soil fertility and pH. One explanation for this unexpected trend is that patterns of forest clearance are not random, and deforestation is likely to have been most severe on the most productive, fertile soils. In many fertile, lowland areas, such as the alluvial lowlands of the West Coast, small remnants are all that

remains of the former forest cover (Fischer & Lindenmayer 2007), and this further emphasises the value of small forest remnants for the conservation of native plant species.

6.3.2 Impacts of exotic plants on native plant species

My study has demonstrated that plant communities in forest fragments have been altered by forest fragmentation, with an increase in the richness and cover of exotic species and a change in the composition of native plant species, particularly at forest edges. What my study does not reveal, however, is whether the invasion of exotic plants has had an impact on native plants in these fragments, or whether changes in the native plant community are purely due to the effects of habitat fragmentation *per se*. I do not know whether exotic plants are directly competing with native species for resources (leading to a decline in some native species), or whether they are simply taking advantage of altered habitat conditions in fragments that native species are not able to exploit. Other authors have also questioned whether invasive species are the drivers of change in ecological communities or simply 'passengers' benefiting from environmental change (Davis 2003; Brown & Sax 2004; Gurevitch & Padilla 2004; Didham *et al.* 2005, see Appendix 8; MacDougall & Turkington 2005).

It seems clear that in some situations invasive species can have major impacts on individuals, populations, and ecosystems (e.g. Vitousek & Walker 1989; Ricciardi 2004; Ricciardi & Atkinson 2004; Yurkonis & Meiners 2004; Clavero & García-Berthou 2005), however not all impacts are negative, and the evidence for a general relationship between the invasiveness of a species and its impact appears to be weak (Ricciardi & Cohen 2007). Relatively few studies have directly measured invader impacts, and much of the evidence linking invasive species to declines in native species is circumstantial (Gurevitch & Padilla 2004; Ricciardi & Cohen 2007). Although invasive plants are commonly listed as threats to native plants in global threat ranking systems (Wilcove *et al.* 1998; IUCN 2008), there have been surprisingly few native plant extinctions documented globally, and there is very little evidence for native plant extinctions being caused directly by invasions of exotic plants (Brown & Sax 2004; Sax & Gaines 2008). These observations highlight the need for more rigorous research on the impacts of invaders on species diversity and ecosystem function. Approaches using both observational and experimental data (involving the addition and removal of exotic species as well as habitat modification), in combination with statistical techniques such as structural equation modeling will be required to improve our understanding of the mechanisms driving native species decline in modified landscapes (Parker *et al.* 1999; Didham *et al.* 2005).

6.3.3 The significance of the extinction debt and invasion debt in fragmented landscapes

It should be remembered that widespread deforestation has occurred relatively recently on the West Coast, and is still ongoing, meaning that the distribution and abundance of plant species in these landscapes may not be at equilibrium with current landscape cover. A recent study in Belgium revealed that an 'extinction debt' persisted for more than 100 years for plant species in forest fragments (Vellend *et al.* 2006). Because many of New Zealand's native plant species have long life spans and slow reproductive rates, it seems likely that there will be a time lag in the responses of native plants to forest fragmentation, and we would expect to see further changes in native species composition and losses of forest-interior specialists over time as the 'extinction debt' is paid out (Tilman *et al.* 1994; Lindborg & Eriksson 2004; Honnay *et al.* 2005; Helm *et al.* 2006; Vellend *et al.* 2006). Similarly, an 'invasion debt' (Seabloom *et al.* 2006) is likely to exist in these recently fragmented landscapes, meaning that populations of naturalised species are likely to continue to expand over time in response to increased human modification of the landscape.

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Appendix 1

Descriptions of the Land Environments of New Zealand (LENZ) classes occupied by the study sites (Leathwick *et al.* 2003a). The codes used in the ordination analyses are shown in brackets.

LENZ class	Landform	Soils	Climate
M1.1a (LENZ75)	Very gently undulating floodplains	Recent, imperfectly drained soils of high fertility from mixed alluvium derived from schist, greywacke and granite alluvium	Mild temperatures, low solar radiation, low vapour pressure deficits, high monthly water balance ratio, no annual water deficits
M2.1a (LENZ94)	Very gently undulating floodplains	Recent, well-drained soils of high fertility from greywacke and granite alluvium	Mild temperatures, moderate solar radiation, low vapour pressure deficits, high monthly water balance ratio, no annual water deficits
O1.4a (LENZ123)	Gently undulating plains	Well-drained soils of moderate fertility from greywacke and granite alluvium	Mild temperatures, moderate solar radiation, low vapour pressure deficits, high monthly water balance ratio, no annual water deficits
O3.1c (LENZ150)	Gently undulating plains	Imperfectly drained soils of moderate fertility from granite and greywacke alluvium	Mild temperatures, with cooler winters, moderate solar radiation, low vapour pressure deficits, high monthly water balance ratio, no annual water deficits
O3.1d (LENZ96)	Gently undulating plains	Imperfectly drained soils of moderate fertility from granite and greywacke alluvium	Mild temperatures, with warmer winters, moderate solar radiation, low vapour pressure deficits, high monthly water balance ratio, no annual water deficits

Appendix 2

Native vascular plant species recorded in this study and number of subplots occupied at each distance from the forest edge (metres). Each 15 x 2 m sampling plot contained three subplots measuring 2 x 5 m each. Negative edge distances indicate plots inside forest, whereas positive edge distances indicate plots in matrix habitat. Note that the number of subplots occupied does not include Forest Control sites. * Species was present at Forest Control sites only.

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Alseuosmiaceae	*Alseuosmia*	*pusilla*		2	3	2	1	2		1					
Apiaceae	*Centella*	*uniflora*	centella			1	4	6	8	10	25	34	33	36	25
Apiaceae	*Hydrocotyle*	*dissecta*	pennywort		4	7	5	7	8	4	7	3	2		
Apiaceae	*Hydrocotyle*	*elongata*	pennywort			3	3	3	3	3	2	2	2	3	
Apiaceae	*Hydrocotyle*	*moschata*	pennywort		1		2	1	4	2	10	3	5	6	
Apiaceae	*Hydrocotyle*	*novae-zelandiae 1*	pennywort (smooth leaf)		1	6	3	3	5	9	16	17	29	24	22
Apiaceae	*Hydrocotyle*	*novae-zelandiae 2*	pennywort (hairy leaf)					1			1	1	1		
Apocynaceae	*Parsonsia*	*heterophylla*	NZ jasmine / kaihua	2	6	19	16	11	12	9	5	1			
Araliaceae	*Pseudopanax*	*crassifolius*	lancewood / horoeka	15	47	73	75	70	62	64	60	11	6	6	1
Araliaceae	*Raukaua*	*simplex*	haumakaroa	6	8	14	11	12	7	5	3				
Araliaceae	*Schefflera*	*digitata*	pate / seven-finger	1	3	8	12	10	6	7	5	3	1	1	
Aspleniaceae	*Asplenium*	*bulbiferum*	hen & chicken's fern	1	7	6	12	7	8	4	1	1			
Aspleniaceae	*Asplenium*	*flaccidum*	hanging spleenwort	12	40	75	88	92	97	105	77	11	6	4	
Aspleniaceae	*Asplenium*	*polyodon*	sickle spleenwort		1	3	5	11	5	3	2	2	1		
Asteraceae	*Euchiton*	*involucratus*	creeping cudweed							3	3	8	15	11	8
Asteraceae	*Lagenifera*	*petiolata*	papataniwhaniwha					2	1	1	2		4	5	
Asteraceae	*Lagenifera*	*pumila*	papataniwhaniwha		3	4	2	6	6	8	5				
Asteraceae	*Leptinella*	*squalida* subsp. *mediana*											3	3	3
Asteraceae	*Leptinella*	*squalida* subsp. *squalida*							1	1		1	1		
Asteraceae	*Olearia*	*arborescens*	tree daisy				1								
Asteraceae	*Pseudognaphalium*	*luteoalbum*	Jersey cudweed											1	
Asteraceae	*Senecio*	*minimus*	native fireweed				1	1	3	6	15	9	8	7	1
Blechnaceae	*Blechnum*	*chambersii*	nini / lance fern			2	2	1	5	4	2	3	1	1	
Blechnaceae	*Blechnum*	*colensoi*	Colenso's hard fern						2	1	2				
Blechnaceae	*Blechnum*	*discolor*	crown fern	18	41	60	45	43	32	30	29	8	4	3	
Blechnaceae	*Blechnum*	*fluviatile*	kiwakiwa / creek fern	2	6	19	21	24	21	19	17	5	3	3	2
Blechnaceae	*Blechnum*	*nigrum*	black hard fern			1									
Blechnaceae	*Blechnum*	*novae-zelandiae*	kiokio	7	19	29	45	57	49	40	53	34	25	12	3
Blechnaceae	*Blechnum*	*penna-marina*	alpine hard fern			5	7	10	7	8	8	4	5	4	
Blechnaceae	*Blechnum*	*procerum*	small kiokio	13	37	47	46	43	33	34	22	8	4	2	1

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Blechnaceae	*Blechnum*	*vulcanicum*	mtn hard fern /korokio			4		8	3	9	7				
Brassicaceae	*Cardamine*	*debilis*	bittercress	3	7	26	37	37	33	34	24	15	8	7	2
Brassicaceae	*Cardamine*	*debilis* "long style"	bittercress		2		1	1		2	1				
Callitrichaceae	*Callitriche*	*muelleri*	native starwort			2		1	1						
Caryophyllaceae	*Stellaria*	*parviflora*	native chickweed		1	2	1								
Chloranthaceae	*Ascarina*	*lucida*	hutu								1				
Cunoniaceae	*Weinmannia*	*racemosa*	kamahi	18	54	74	76	82	71	70	59	29	8	5	
Cupressaceae	*Libocedrus*	*bidwillii*	pahautea / kaikawaka	1	2	5	3	2	5	5	5				
Cyatheaceae	*Cyathea*	*smithii*	soft tree fern / katote	9	33	43	43	28	27	21	11	6	2	2	
Cyperaceae	*Baumea*	*rubiginosa*	sedge tussock											2	3
Cyperaceae	*Baumea*	*tenax*	sedge tussock						1	1	2				
Cyperaceae	*Carex*	*coriacea*	rautahi	2				3	2	4	5	5	2	7	4
Cyperaceae	*Carex*	*dissita*				3	6	9	13	9	13	7	6	6	2
Cyperaceae	*Carex*	*gaudichaudiana*						3	1			3	6	6	4
Cyperaceae	*Carex*	*geminata*		1	3	3	5	4	5	7	15	18	16	12	9
Cyperaceae	*Carex*	*sinclairii*					2			3	4	9	7	10	5
Cyperaceae	*Carex*	*virgata*							1	2	1	3	3		1
Cyperaceae	*Eleocharis*	*gracilis*	slender spike sedge										5	8	8
Cyperaceae	*Isolepis*	*habra*	club sedge						4	1		1	2	1	
Cyperaceae	*Isolepis*	*prolifer*	club sedge						1		1	4	7	3	3
Cyperaceae	*Isolepis*	*subtilissima*	club sedge								2	3	5	3	3
Cyperaceae	*Uncinia*	*angustifolia*	hook grass		8	13	8	7	6	5	3	2			
Cyperaceae	*Uncinia*	*distans*	hook grass	3	2	7	6	6	6	7	5				
Cyperaceae	*Uncinia*	*ferruginea*	hook grass	3	1	4	4	3	3	3	3	3			
Cyperaceae	*Uncinia*	*gracilenta*	hook grass	2	8	4	5	7	7	5	5	1			
Cyperaceae	*Uncinia*	*laxiflora*	hook grass	1											
Cyperaceae	*Uncinia*	*rupestris*	hook grass			1	2	1	2	1					
Cyperaceae	*Uncinia*	*spp.*	hook grass		10	22	19	18	16	8	9	2	1	1	
Cyperaceae	*Uncinia*	*uncinata*	hook grass	7	13	17	15	16	15	14	12	2		2	
Dennstaedtiaceae	*Hypolepis*	*ambigua*			4	9	16	17	13	18	17	6	7	5	3
Dennstaedtiaceae	*Hypolepis*	*distans*									2				
Dennstaedtiaceae	*Hypolepis*	*lactea*			2	1	2	5	3	4	4	2	1	3	
Dennstaedtiaceae	*Hypolepis*	*millefolium*	thousand-leaved fern			2					3	2	2		1
Dennstaedtiaceae	*Hypolepis*	*rufobarbata*	sticky pig fern		7	9	8	12	12	15	10	3	2	2	1
Dennstaedtiaceae	*Leptolepia*	*novae-zelandiae*	lace fern			2									
Dennstaedtiaceae	*Lindsaea*	*trichomanoides*		1	1	2	3								
Dicksoniaceae	*Dicksonia*	*fibrosa*	wheki-ponga				1								

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				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Dicksoniaceae	*Dicksonia*	*squarrosa*	wheki	9	45	60	65	64	53	48	56	22	13	8	1
Dryopteridaceae	*Deparia*	*petersenii*					1								
Dryopteridaceae	*Lastreopsis*	*glabella*	smooth shield fern				1								
Dryopteridaceae	*Lastreopsis*	*hispida*	hairy fern			1	2								
Dryopteridaceae	*Polystichum*	*vestitum*	prickly shield fern	3	16	34	38	36	42	42	41	19	18	3	4
Dryopteridaceae	*Rumohra*	*adiantiformis*	leathery shield fern		3	3	6	10	7	2	3				
Elaeocarpaceae	*Aristotelia*	*serrata*	wineberry / makomako	2	16	36	42	30	33	33	36	17	10	7	1
Elaeocarpaceae	*Elaeocarpus*	*dentatus*	hinau	1	3	5	9	7	9	6	7	2			
Elaeocarpaceae	*Elaeocarpus*	*hookerianus*	pokaka	16	41	60	42	38	44	35	30	8		1	
Epacridaceae	*Archeria*	*traversii*		1											
Epacridaceae	*Cyathodes*	*juniperina*	prickly mingimingi		1				1						
Epacridaceae	*Leucopogon*	*fasciculatus*	mingimingi	6	14	26	32	31	37	39	30	10	3	1	
Ericaceae	*Gaultheria*	*antipoda*	fool's beech / snowberry		1			1							
Escalloniaceae	*Carpodetus*	*serratus*	marbleleaf / putaputaweta	2	13	22	32	31	25	33	35	13	6	2	
Escalloniaceae	*Quintinia*	*acutifolia*	Westland quintinia	7	25	34	27	24	17	18	15	4	2		
Fabaceae	*Carmichaelia*	*australis*	broom			2	5	6	6	3	3	2	1		
Fagaceae	*Nothofagus*	*fusca*	red beech	18	29	56	58	58	61	59	58	39	17	8	1
Fagaceae	*Nothofagus*	*fusca x solandri* var. *solandri*										1			
Fagaceae	*Nothofagus*	*menziesii*	silver beech	9	21	33	37	40	43	41	40	23	10	2	1
Fagaceae	*Nothofagus*	*solandri var. solandri*	black beech	3	7	15	14	8	11	13	12	4	2	1	
Fagaceae	*Nothofagus*	*truncata*	hard beech	7	9	12	13	11	10	12	7	5	1		
Gleicheniaceae	*Gleichenia*	*microphylla*	tangle fern / waewaekaka			2			1	2	4	1	1	2	1
Gleicheniaceae	*Sticherus*	*cunninghamii*	umbrella fern	3	4	2									
Grammitidaceae	*Ctenopteris*	*heterophylla*		16	40	65	64	60	50	38	20				
Grammitidaceae	*Grammitis*	*billiardieri*	strap fern	20	49	93	94	92	74	63	38	1		1	
Griseliniaceae	*Griselinia*	*littoralis*	broadleaf / papauma	22	48	74	83	79	69	68	64	15	6	3	2
Haloragaceae	*Gonocarpus*	*aggregatus*					1								
Haloragaceae	*Gonocarpus*	*micranthus*									2	3	5	9	12
Haloragaceae	*Gunnera*	*prorepens*	gunnera										3	4	5
Hymenophyllaceae	*Hymenophyllum*	*bivalve*	filmy fern	13	29	46	51	48	35	34	15		1	1	
Hymenophyllaceae	*Hymenophyllum*	*demissum*	filmy fern	9	21	26	22	14	9	5	2				
Hymenophyllaceae	*Hymenophyllum*	*dilatatum*	filmy fern / matua mauku		2	5	6	6	2	1	3				
Hymenophyllaceae	*Hymenophyllum*	*flabellatum*	fan-like filmy fern	1	6	18	16	13	5	1	1				
Hymenophyllaceae	*Hymenophyllum*	*lyallii*	filmy fern		1	3	2	2	4	2					
Hymenophyllaceae	*Hymenophyllum*	*malingii*	filmy fern		2										
Hymenophyllaceae	*Hymenophyllum*	*multifidum*	filmy fern	1	2	6	5	4	1	2	1				

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Hymenophyllaceae	*Hymenophyllum*	*pulcherrimum*	filmy fern			1	2		1						
Hymenophyllaceae	*Hymenophyllum*	*rarum*	filmy fern	1	1	5	3	6	2	1					
Hymenophyllaceae	*Hymenophyllum*	*revolutum*	filmy fern	9	18	33	29	19	12	6	1				
Hymenophyllaceae	*Hymenophyllum*	*sanguinolentum*	piripiri / filmy fern	4	2	16	13	7	2	2	1				
Hymenophyllaceae	*Hymenophyllum*	*scabrum*	filmy fern		2	8	2	4	2	2					
Hymenophyllaceae	*Hymenophyllum*	*villosum*	filmy fern	10	30	45	42	39	31	22	18	1			
Hymenophyllaceae	*Trichomanes*	*reniforme*	kidney fern / raurenga	1											
Icacinaceae	*Pennantia*	*corymbosa*	kaikomako		4	18	12	12	11	16	12	6	6	1	1
Iridaceae	*Libertia*	*micrantha*	NZ iris	5	9	12	5	4	3	3					
Juncaceae	*Juncus*	*edgariae*										3	4	7	10
Juncaceae	*Juncus*	*planifolius*							1			1	2	4	1
Juncaceae	*Juncus*	*sarophorus*							1	3	16	16	22	22	21
Juncaceae	*Luzula*	*banksiana*	woodrush			1				2	2	1			
Juncaceae	*Luzula*	*picta* var. *limosa*	woodrush									1	1	1	
Liliaceae	*Astelia*	*fragrans*	kauri grass		4	2	1	2	1	4	2	1			
Liliaceae	*Astelia*	*grandis*	large kauri grass						1	1					
Liliaceae	*Dianella*	*nigra*	NZ blueberry / turutu		2	5	6	13	18	11	10	8	6		
Liliaceae	*Luzuriaga*	*parviflora*	lanternberry	6	11	17	16	12	3	2	3				
Lobeliaceae	*Pratia*	*angulata*	pratia	2		1	7	3	2	4	3	7	8	8	4
Lycopodiaceae	*Lycopodium*	*scariosum*	creeping clubmoss												
Lycopodiaceae	*Lycopodium*	*varium*	creeping clubmoss		2	3	3		5	2	1				
Lycopodiaceae	*Lycopodium*	*volubile*	climbing clubmoss		1	1		2	1	4	4	2	1	2	
Malvaceae	*Hoheria*	*glabrata*	mountain lacebark			4	3	2	1	1	1				
Monimiaceae	*Hedycarya*	*arborea*	pigeonwood	1	4	5	5	3	3	1	1				
Moraceae	*Streblus*	*heterophyllus*	milk tree / turepo			1	1								
Myrsinaceae	*Myrsine*	*australis*	red matipo	8	15	27	30	30	21	24	19	5	1		
Myrsinaceae	*Myrsine*	*divaricata*		14	47	75	81	71	56	70	49	12	5	2	2
Myrsinaceae	*Myrsine*	*salicina*	toro	4	14	10	15	11	8	6	6	2			
Myrsinaceae	*Myrsine*	*salicina x divaricata*				2	4	1	5	1		1			
Myrtaceae	*Kunzea*	*ericoides*	kanuka				1	5	7	10	14	10	8	3	1
Myrtaceae	*Leptospermum*	*scoparium*	manuka		5	1		2	1	3	5	4	2	2	2
Myrtaceae	*Metrosideros*	*diffusa*	white climbing rata	10	25	31	27	26	28	20	19	6	1	1	
Myrtaceae	*Metrosideros*	*perforata*	aka						1	1					
Myrtaceae	*Metrosideros*	*umbellata*	southern rata						1						
Myrtaceae	*Neomyrtus*	*pedunculata*	rohutu	22	63	103	116	104	112	104	90	33	14	5	1
Onagraceae	*Epilobium*	*brunnescens*	native willowherb										1		3
Onagraceae	*Epilobium*	*chionanthum*	native willowherb										1		

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				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Onagraceae	*Epilobium*	*pedunculare*	creeping willowherb		1			2	3	5	3	1	2	1	1
Onagraceae	*Fuchsia*	*excorticata*	tree fuchsia		10	9	4	9	18	14	24	15	9	4	
Onagraceae	*Fuchsia*	*excorticata x perscandens*	shrubby fuchsia	2		5	3	2	3	3					
Ophioglossaceae	*Ophioglossum*	*coriaceum*	adder's tongue									1			
Orchidaceae	*Adenochilus*	*gracilis*	slender forest orchid		3	1	1	3	1	2	1				
Orchidaceae	*Aporostylis*	*bifolia*	odd-leaved orchid	1	2	1	2								
Orchidaceae	*Caladenia*	*catenata*	pink orchid		3		3								
Orchidaceae	*Chiloglottis*	*cornuta*	ant orchid	1	1	1	1	1							
Orchidaceae	*Corybas*	*cheesemanii*	monks-hood flower			1									
Orchidaceae	*Corybas*	*macranthus*	spider orchid			1									
Orchidaceae	*Corybas*	*oblongus*	spider orchid		1	1									
Orchidaceae	*Corybas*	*rivularis*	spider orchid	2	2	1	3								
Orchidaceae	*Corybas*	*trilobus*	spider orchid		2	10	6	2	1						
Orchidaceae	*Drymoanthus*	*adversus*			1	1	2	3	1						
Orchidaceae	*Earina*	*autumnalis*	easter orchid		1	2	3	1	1	1	1				
Orchidaceae	*Earina*	*mucronata*	peka-a-waka		1	2	1	4	1	2					
Orchidaceae	*Gastrodia*	*cunninghamii*	potato orchid / huperei				1								
Orchidaceae	*Microtis*	*unifolia*	onion orchid				1			1		2	4	1	2
Orchidaceae	*Pterostylis*	sp.	green hooded orchid		3	1	3	4	3	1	1				
Orchidaceae	*Winika*	*cunninghamii*	lady's slipper orchid				1								
Osmundaceae	*Leptopteris*	*hymenophylloides*		3				2							
Osmundaceae	*Leptopteris*	*superba*	Prince of Wales' feathers	1	6	4	5	4	4	2		1	1	1	
Pittosporaceae	*Pittosporum*	*colensoi*			5	10	6	9	9	11	11	1		1	
Pittosporaceae	*Pittosporum*	*eugenioides*	lemonwood / tarata								1				
Pittosporaceae	*Pittosporum*	*rigidum*			2	2	6	1	1	1	1				
Plantaginaceae	*Gratiola*	*nana*						1							
Plantaginaceae	*Hebe*	*salicifolia*								1	1				
Poaceae	*Cortaderia*	*richardii*	toetoe								1				
Poaceae	*Microlaena*	*avenacea*	bush rice grass	11	25	34	43	30	24	24	19	7	2	1	
Podocarpaceae	*Dacrycarpus*	*dacrydioides*	kahikatea	13	42	92	93	90	85	79	62	35	15	8	2
Podocarpaceae	*Dacrydium*	*cupressinum*	rimu	13	34	48	49	51	50	43	41	14	2	2	
Podocarpaceae	*Halocarpus*	*biformis*	pink pine		1	4	1	2	3	3	1				
Podocarpaceae	*Manoao*	*colensoi*	silver pine / manoao		5	4	4	3	6	7	2				
Podocarpaceae	*Phyllocladus*	*alpinus*	mtn celery pine / toatoa	10	29	46	48	49	43	42	41	15	2		
Podocarpaceae	*Podocarpus*	*acutifolius*	sharp-leaved totara			4	8	6	10	13	12	6	1	1	
Podocarpaceae	*Podocarpus*	*hallii*	halls totara	2	7	9	10	14	10	11	9	4	2		

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				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Podocarpaceae	*Podocarpus*	*totara*	totara	4	8	21	20	30	22	19	20	15	4	3	
Podocarpaceae	*Prumnopitys*	*ferruginea*	miro	24	58	87	75	76	63	61	33	7	3	1	1
Podocarpaceae	*Prumnopitys*	*taxifolia*	matai				6	5	2	4	2				
Polygonaceae	*Muehlenbeckia*	*australis*	large-leaved pohuehue	4	12	28	29	31	41	38	41	18	11	7	4
Polypodiaceae	*Microsorum*	*pustulatum*	hound's tongue		11	31	54	44	48	48	38	5			2
Polypodiaceae	*Pyrrosia*	*eleagnifolia*	leather leaf fern			3	7	10	13	9	14	2			
Psilotaceae	*Tmesipteris*	*elongata*	fork fern		2	4	5	6	5	6	4				
Psilotaceae	*Tmesipteris*	*tannensis*	fork fern		6			1	1						
Pteridiaceae	*Histiopteris*	*incisa*	water fern		16	19	27	36	40	38	49	31	24	21	10
Pteridiaceae	*Paesia*	*scaberula*	ring fern		1	1	8	12	13	29	48	45	34	20	6
Pteridiaceae	*Pteridium*	*esculentum*	bracken / rarauhe			4	6	18	45	64	86	66	48	29	13
Ranunculaceae	*Clematis*	*paniculata*	puawhananga		5	7	5	6	3		3	1			
Ranunculaceae	*Ranunculus*	*foliosus*	native buttercup		1										
Ranunculaceae	*Ranunculus*	*reflexus*	hairy buttercup / maruru		1	3	2	1	2						
Rosaceae	*Acaena*	*anserinifolia*	bidibidi	2	2	9	13	16	22	30	39	30	21	14	3
Rosaceae	*Rubus*	*australis*	small bush lawyer	14	43	65	65	66	56	61	58	29	13	5	2
Rosaceae	*Rubus*	*cissoides*	bush lawyer	3	4	4	5	9	6	6	4	2	1		
Rosaceae	*Rubus*	*schmidelioides*	bush lawyer			4	1	3	5	4	5	1	1		
Rubiaceae	*Coprosma*	*ciliata*		2	12	17	17	7	9	10	7	1			
Rubiaceae	*Coprosma*	*colensoi*		2	10	10	9	4	5	4				1	
Rubiaceae	*Coprosma*	*foetidissima*	stinkwood	12	29	45	30	31	18	12	13	2			
Rubiaceae	*Coprosma*	*grandifolia*	karamu	3	4	5	10	9	6	1	1				
Rubiaceae	*Coprosma*	*lucida*	karamu		5	4	7	1	6	5		1			
Rubiaceae	*Coprosma*	*propinqua*	mingimingi / black scrub	1	12	27	53	42	63	64	71	43	17	12	4
Rubiaceae	*Coprosma*	*pseudocuneata*				1									
Rubiaceae	*Coprosma*	*rhamnoides*		7	11	27	24	27	26	28	26	12	7	5	
Rubiaceae	*Coprosma*	*rigida*				3	5	3	4	8	4	3	1		
Rubiaceae	*Coprosma*	*robusta x propinqua*					1	2	1	4	8	8			
Rubiaceae	*Coprosma*	*rotundifolia*	round-leaved coprosma	3	10	34	45	38	41	42	32	19	10	3	
Rubiaceae	*Coprosma*	*rugosa*					1			1	1	1			
Rubiaceae	*Coprosma*	*tayloriae*		27	68	105	113	115	111	118	124	74	44	23	10
Rubiaceae	*Coprosma*	*tenuicaulis*	hukihuki	5	9	19	29	26	20	22	12	5	1	1	1
Rubiaceae	*Nertera*	*depressa*		8	38	61	68	57	56	55	47	24	18	10	5
Rubiaceae	*Nertera*	*villosa*		20	44	56	40	34	25	23	16	3	4	1	
Rutaceae	*Melicope*	*simplex*	poataniwha	7	21	43	39	32	29	25	14	2	1	2	
Scrophulariaceae	*Mazus*	*radicans*				1									
Smilacaceae	*Ripogonum*	*scandens*	supplejack	2	6	11	14	10	7	2	1	1			

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Thelypteridaceae	*Pneumatopteris*	*pennigera*	gully fern						1	1					
Urticaceae	*Urtica*	*incisa*	small stinging nettle			3		2	1	3	1	1	1		
Violaceae	*Melicytus*	*lanceolatus*	mahoe wao			2		3	2	2	1		1		
Violaceae	*Melicytus*	*ramiflorus*	mahoe / whiteywood		1	2	2	3	4	3	3				
Violaceae	*Viola*	*filicaulis*	violet			7	9	3	1	2		1	1	3	
Violaceae	*Viola*	*lyallii*	violet		2	5	10	7	12	16	19	20	18	15	12
Winteraceae	*Pseudowintera*	*colorata*	horopito / pepper tree	20	41	81	82	76	67	66	47	13	7	2	1
Total number of subplots at each distance from the forest edge				**30**	**75**	**123**	**132**	**132**	**132**	**132**	**132**	**132**	**129**	**120**	**108**

Appendix 3

Exotic vascular plant species recorded in this study and number of subplots occupied at each distance from the forest edge (metres). Each 15 x 2 m sampling plot contained three subplots measuring 2 x 5 m each. Negative edge distances indicate plots inside forest, whereas positive edge distances indicate plots in matrix habitat. Note that the number of subplots occupied does not include Matrix Control sites. * Species was present at Matrix Control sites only.

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Aquifoliaceae	*Ilex*	*aquifolium*	holly							1	2	3	5	5	5
Araliaceae	*Hedera*	*helix*	ivy								1	5	7	4	2
Asteraceae	*Achillea*	*millefolium*	yarrow												*
Asteraceae	*Bellis*	*perennis*	common lawn daisy								1	3	5	5	3
Asteraceae	*Bidens*	*tripartita*	swamp beggar's ticks						1		1				
Asteraceae	*Cichorium*	*intybus*	chicory								1	5	7	4	2
Asteraceae	*Cirsium*	*arvense*	Californian thistle								1	1		1	
Asteraceae	*Cirsium*	*palustre*	marsh thistle		2	1	1	5	12	15	28	34	35	25	22
Asteraceae	*Cirsium*	*vulgare*	Scotch thistle						1			6	4	7	6
Asteraceae	*Crepis*	*capillaris*	hawksbeard							1	2	3	5	5	5
Asteraceae	*Gamochaeta*	*spicata*	purple cudweed					1		3	11	25	26	33	29
Asteraceae	*Hypochaeris*	*radicata*	catsear					1	3	1		1			
Asteraceae	*Lapsana*	*communis*	nipplewort						1	2		1			
Asteraceae	*Leontodon*	*taraxacoides*	hawkbit							2		6	12	8	8
Asteraceae	*Leucanthemum*	*vulgare*	ox-eye daisy											1	
Asteraceae	*Matricaria*	*dioscoidea*	pineapple mayweed												*
Asteraceae	*Mycelis*	*muralis*	wall lettuce			15	19	20	20	16	12	2	3	4	
Asteraceae	*Senecio*	*jacobaea*	ragwort			1		1	1	10	19	22	24	17	13
Asteraceae	*Sonchus*	*asper*	prickly sow thistle / puha										1	1	
Asteraceae	*Sonchus*	*oleraceus*	smooth sow thistle / puha									1	1		
Asteraceae	*Taraxacum*	*officinale*	dandelion									5	5	6	7
Boraginaceae	*Myosotis*	*arvensis*	field forget-me-not									1			
Brassicaceae	*Brassica*	*rapa*	turnip / fodder crop											1	1
Brassicaceae	*Capsella*	*bursa-pastoris*	shepherd's purse												*
Callitrichaceae	*Callitriche*	*stagnalis*	starwort									1	1	1	
Caprifoliaceae	*Leycesteria*	*formosa*	Himalayan honeysuckle							4	8	8	6	4	1
Caryophyllaceae	*Cerastium*	*fontanum*	mouse-ear chickweed			1				4	17	21	29	30	25
Caryophyllaceae	*Cerastium*	*glomeratum*	annual mouse-ear chickweed				1	1	3	8	20	17	16	17	22
Caryophyllaceae	*Sagina*	*procumbens*	procumbent pearlwort										2	5	6
Caryophyllaceae	*Stellaria*	*graminea*	stitchwort							1	1	9	14	9	18
Caryophyllaceae	*Stellaria*	*media*	chickweed			2	1	3	1	2	12	11	6	9	5

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Clusiaceae	*Hypericum*	*androsaemum*	tutsan		2	1	1	5	12	15	28	34	35	25	22
Clusiaceae	*Hypericum*	*humifusum*	trailing St John's wort						1			6	4	7	6
Cupressaceae	*Cupressus*	*macrocarpa*	macrocarpa				1		1	1	1				
Cyperaceae	*Carex*	*demissa*									2	3	4	5	4
Cyperaceae	*Carex*	*ovalis*	oval sedge					1		3	11	25	26	33	29
Dryopteridaceae	*Dryopteris*	*dilatata*	broad buckler fern		2	3	9	13	17	11	11	1	1	2	
Ericaceae	*Erica*	*lusitanica*	Spanish heath								1		1		
Fabaceae	*Cytisus*	*scoparius*	broom						1	4	5	2			
Fabaceae	*Lotus*	*pedunculatus*	lotus				2	4	4	15	67	80	86	82	68
Fabaceae	*Lotus*	*suaveolens*	hairy birdsfoot trefoil									1	2	1	1
Fabaceae	*Trifolium*	*dubium*	suckling clover									3	3	2	2
Fabaceae	*Trifolium*	*pratense*	red clover								2	9	18	14	8
Fabaceae	*Trifolium*	*repens*	white clover				1		2	4	30	52	60	68	62
Fabaceae	*Ulex*	*europaeus*	gorse		2		3	5	21	44	66	54	51	39	26
Geraniaceae	*Geranium*	*robertianum*	herb Robert			1				4	17	21	29	30	25
Iridaceae	*Crocosmia*	*x crocosmiiflora*	montbretia										2		
Juncaceae	*Juncus*	*acuminatus*	sharp-fruited rush										2		
Juncaceae	*Juncus*	*acutiflorus*	sharp-flowered rush				1		1	1	1				
Juncaceae	*Juncus*	*articulatus*	jointed rush								1	2	3	4	5
Juncaceae	*Juncus*	*bufonius*	toad rush						1	4	5	2			
Juncaceae	*Juncus*	*bulbosus*	bulbous rush							2	12	17	21	13	8
Juncaceae	*Juncus*	*canadensis*	tailed-seed rush								2	2	1	1	1
Juncaceae	*Juncus*	*effusus*	soft rush		2	2	8	13	20	47	70	53	36	22	9
Juncaceae	*Juncus*	*ensifolius*	iris-leaved rush		2	3	9	13	17	11	11	1	1	2	
Juncaceae	*Juncus*	*tenuis*	slender rush						1	1		1	2	9	3
Juncaceae	*Luzula*	*congesta*	woodrush						1	1	4	2	2	4	1
Lamiaceae	*Mentha*	*pulegium*	penny royal										1	1	2
Lamiaceae	*Prunella*	*vulgaris*	selfheal		1	3	8	9	7	16	47	47	55	59	51
Lamiaceae	*Stachys*	*sylvatica*	hedge woundwort						1						
Lythraceae	*Lythrum*	*hyssopifolia*	hyssop loosestrife											1	
Lythraceae	*Lythrum*	*portula*	water purslane									4	5	9	7
Onagraceae	*Epilobium*	*ciliatum*	tall willow-herb						1	1		1	2	9	3
Onagraceae	*Ludwigia*	*palustris*											1	1	
Orobanchaceae	*Orobanche*	*minor*	broomrape											1	
Plantaginaceae	*Plantago*	*lanceolata*	narrow-leaved plantain					1			7	33	37	36	42
Plantaginaceae	*Plantago*	*major*	broad-leaved plantain					2	2	2	2	9	14	22	20
Poaceae	*Agrostis*	*capillaris*	brown top				2	1	6	14	51	65	66	74	68

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Poaceae	*Anthoxanthum*	*odoratum*	sweet vernal			3	5	6	13	24	67	70	73	72	59
Poaceae	*Cynosurus*	*cristatus*	crested dog's tail								1	2	3	4	5
Poaceae	*Dactylis*	*glomerata*	cocksfoot							2	12	17	21	13	8
Poaceae	*Danthonia*	*decumbens*	heath grass								2	2	1	1	1
Poaceae	*Glyceria*	*declinata*	glaucous sweet grass				1	1	3	8	20	17	16	17	22
Poaceae	*Holcus*	*lanatus*	yorkshire fog								1	1		1	
Poaceae	*Lolium*	*multiflorum*	Italian ryegrass									1			
Poaceae	*Lolium*	*perenne*	ryegrass							2	4	22	37	37	39
Poaceae	*Phleum*	*pratense*	timothy										5	4	4
Poaceae	*Poa*	*annua*	annual poa									3	5	8	11
Poaceae	*Poa*	*pratensis*													*
Polygonaceae	*Acetosa*	*acetosella*	sheep's sorrel						1	3	7	9	6	4	5
Polygonaceae	*Persicaria*	*hydropiper*	water pepper			1		1	4	6	10	20	25	29	22
Polygonaceae	*Rumex*	*conglomeratus*	clustered dock										1		
Polygonaceae	*Rumex*	*crispus*	curled dock									1	2	9	9
Polygonaceae	*Rumex*	*obtusifolius*	broad-leaved dock			1	2	2	2	5	5	28	31	33	37
Ranunculaceae	*Ranunculus*	*acris*	giant buttercup										1	1	
Ranunculaceae	*Ranunculus*	*flammula*	spearwort									1	2	2	
Ranunculaceae	*Ranunculus*	*repens*	creeping buttercup	1		2	6	10	14	29	71	93	93	85	71
Rosaceae	*Crataegus*	*monogyna*	hawthorn					1	3	1		1			
Rosaceae	*Fragaria*	*vesca*	alpine strawberry									1	1	1	
Rosaceae	*Potentilla*	*anglica*	creeping cinquefoil				1	1	1	2	4	13	15	21	16
Rosaceae	*Prunus*	*avium*	cherry				1				1				
Rosaceae	*Prunus*	*laurocerasus*	cherry laurel					1							
Rosaceae	*Rubus*	*fruticosus*	blackberry			5	6	9	32	46	47	46	38	31	13
Rosaceae	*Rubus*	*laciniatus*	cut-leaved blackberry		1					1	2	1			2
Rosaceae	*Sorbus*	*aucuparia*	rowan		2	4	2	6	4	3	5	2		1	
Rubiaceae	*Galium*	*aparine*	cleavers							1	1				
Rubiaceae	*Galium*	*palustre*	marsh bedstraw								2	3	4	5	4
Rubiaceae	*Sherardia*	*arvensis*	field madder												*
Scrophulariaceae	*Digitalis*	*purpurea*	foxglove		2	2	8	13	20	47	70	53	36	22	9
Scrophulariaceae	*Mimulus*	*guttatus*	monkey musk											1	2
Scrophulariaceae	*Mimulus*	*moschatus*	musk								1	2	3	2	1
Scrophulariaceae	*Parentucellia*	*viscosa*	tarweed								1	3	7	7	7
Scrophulariaceae	*Veronica*	*arvensis*	field speedwell								2	5	3	6	3
Scrophulariaceae	*Veronica*	*scutellata*	marsh speedwell										1		
Scrophulariaceae	*Veronica*	*serpyllifolia*	turf speedwell									6	8	13	13

Family	Genus	species	Common name/s	Number of subplots occupied at each distance from the forest edge (m)											
				Forest								Matrix			
				-128	-64	-32	-16	-8	-4	-2	-0.3	0.3	2	4	8
Solanaceae	*Solanum*	*chenopodioides*	velvety nightshade			3	2	2	5	7	15	5			
Solanaceae	*Solanum*	*dulcamara*	bittersweet								1	1			
Solanaceae	*Solanum*	*nigrum*	black nightshade											3	
Total number of subplots at each distance from the forest edge				**30**	**75**	**123**	**132**	**132**	**132**	**132**	**132**	**132**	**129**	**120**	**108**

Appendix 4

Pearson correlations (R^2) between the treatment variables and the other environmental variables used in ordination analyses. Codes for variables are given in **Chapter 2, Table 2.2**. Significance level: *** = p <0.001, ** = p <0.01, * = p <0.05, NS = non-significant (p >0.05). N = 516.

	Landscap		LogArea		Edgedist		LscpArea		LscpEdge		AreaEdge		LxAxE	
	R^2	**P**	**R^2**	**P**	**R^2**	**P**	**R^2**	**P**	**R^2**	**P**	**R^2**	**P**	**R^2**	**P**
ShapeInd	0.80	***	0.89	***	-0.60	***	0.98	***	-0.91	***	-0.96	***	-0.99	***
Canopy	0.33	***	0.32	***	-0.80	***	0.23	***	-0.45	***	-0.31	***	-0.22	***
beef	0.03	NS	-0.13	**	0.02	NS	-0.09	*	0.07	NS	0.09	*	0.09	NS
dairy	-0.37	***	-0.31	***	0.26	***	-0.30	***	0.27	***	0.26	***	0.26	***
deer	0.04	NS	0.07	NS	0.00	NS	-0.03	NS	0.07	NS	0.09	NS	0.10	*
sheepbef	-0.07	NS	-0.08	NS	0.00	NS	-0.10	*	0.08	NS	0.09	*	0.10	*
Grazing	-0.27	***	-0.33	***	0.62	***	-0.28	***	0.43	***	0.34	***	0.28	***
Baregrnd	-0.05	NS	0.00	NS	0.06	NS	-0.01	NS	0.04	NS	0.03	NS	0.02	NS
Moss	0.50	***	0.49	***	-0.60	***	0.54	***	-0.65	***	-0.60	***	-0.57	***
RaisedM	0.40	***	0.25	***	-0.39	***	0.29	***	-0.38	***	-0.32	***	-0.30	***
DeadTree	0.16	***	0.14	**	-0.22	***	0.16	***	-0.21	***	-0.19	***	-0.17	***
LiveTree	0.21	***	0.21	***	-0.49	***	0.20	***	-0.36	***	-0.28	***	-0.23	***
WeedTree	-0.09	*	-0.01	NS	0.10	*	-0.05	NS	0.10	*	0.08	NS	0.06	NS
TreeDiv	0.20	***	0.18	***	-0.57	***	0.15	**	-0.36	***	-0.25	***	-0.18	***
DACcup	-0.06	NS	-0.01	NS	-0.13	**	-0.05	NS	-0.02	NS	0.01	NS	0.04	NS
DACdac	-0.06	NS	-0.13	**	-0.06	NS	-0.10	*	0.03	NS	0.07	NS	0.08	NS
NOTfus	0.13	**	0.00	NS	-0.19	***	-0.02	NS	-0.06	NS	0.01	NS	0.04	NS
NOTmen	-0.07	NS	-0.09	NS	-0.12	*	-0.10	*	0.00	NS	0.06	NS	0.08	NS
NOTtru	0.45	***	0.56	***	-0.40	**	0.57	***	-0.54	***	-0.57	***	-0.56	***
QUIacu	-0.01	NS	0.13	**	-0.20	***	0.04	NS	-0.10	*	-0.09	*	-0.04	NS
WEIrac	0.15	**	0.21	***	-0.35	***	0.18	***	-0.27	***	-0.24	***	-0.19	***
SaplingD	0.29	***	0.28	***	-0.59	***	0.25	***	-0.42	***	-0.33	***	-0.27	***
SaplingN	0.31	***	0.30	***	-0.47	***	0.30	***	-0.40	***	-0.34	***	-0.31	***
SoilpH	-0.45	***	-0.46	***	0.54	***	-0.41	***	0.44	***	0.39	***	0.38	***
SoilP	-0.27	***	-0.24	***	0.37	***	-0.20	***	0.21	***	0.17	***	0.17	***
SoilOM	0.11	*	0.13	**	-0.19	***	0.11	*	-0.14	**	-0.12	**	-0.11	*
SoilN	-0.05	NS	-0.10	*	-0.02	NS	-0.09	*	0.04	NS	0.06	NS	0.06	NS
SoilCN	0.64	***	0.72	***	-0.60	***	0.67	***	-0.63	***	-0.62	***	-0.62	***
Tmin	-0.60	***	-0.32	***	0.28	***	-0.41	***	0.39	***	0.37	***	0.38	***
JuneS	-0.37	***	-0.14	**	0.08	NS	-0.24	***	0.22	***	0.22	***	0.23	***
Vpd	-0.25	***	-0.28	***	0.18	***	-0.28	***	0.25	***	0.26	***	0.27	***
R2pet	-0.24	***	-0.01	NS	0.04	NS	-0.12	**	0.13	**	0.12	**	0.13	**
LENZ75	-0.04	NS	-0.07	NS	***	NS	-0.05	NS	0.03	NS	0.04	NS	0.04	NS
LENZ94	-0.21	***	-0.12	**	0.14	**	-0.10	*	0.09	NS	0.07	NS	0.07	NS
LENZ96	-0.03	NS	-0.10	*	***	NS	-0.08	NS	0.06	NS	0.08	NS	0.07	NS
LENZ123	-0.22	***	-0.27	***	0.21	***	-0.34	***	0.33	***	0.35	***	0.37	***
LENZ150	0.46	***	0.54	***	-0.38	***	0.60	***	-0.56	***	-0.59	***	-0.61	***
Drainage	-0.48	***	-0.42	***	0.39	***	-0.51	***	0.50	***	0.50	***	0.52	***
NND	0.56	***	0.76	***	-0.47	***	0.82	***	-0.75	***	-0.81	***	-0.83	***
NearRoad	-0.16	***	-0.11	*	0.05	NS	-0.13	**	0.11	*	0.12	**	0.12	**
NearRiv	0.28	***	0.18	***	-0.15	**	0.20	***	-0.19	***	-0.18	***	-0.18	***
NearBuil	0.72	***	0.66	***	-0.48	***	0.71	***	-0.65	***	-0.67	***	-0.69	***
FNum256	-0.03	NS	-0.27	***	0.03	NS	-0.19	***	0.14	**	0.16	***	0.15	**
FNum512	-0.23	***	-0.31	***	0.13	***	-0.30	***	0.25	***	0.27	***	0.27	***
FNum1024	-0.30	***	-0.36	***	0.12	*	-0.39	***	0.33	***	0.37	***	0.37	***
FNum2046	-0.29	***	-0.29	***	0.18	***	-0.34	***	0.32	***	0.34	***	0.34	***
FNum4096	-0.37	***	-0.24	***	0.18	***	-0.35	***	0.34	***	0.34	***	0.36	***
FNum8192	-0.42	***	-0.34	***	0.22	***	-0.42	***	0.39	***	0.40	***	0.42	***
Edge256	-0.17	***	-0.40	***	0.09	*	-0.42	***	0.35	***	0.42	***	0.43	***
Edge512	-0.10	*	-0.27	***	0.08	NS	-0.32	***	0.29	***	0.34	***	0.35	***
Edge1024	-0.14	**	-0.22	***	0.07	NS	-0.33	***	0.32	***	0.36	***	0.39	***

Edge2048	-0.11	*	-0.23	***	0.06	NS	-0.35	***	0.33	***	0.39	***	0.41	***
Edge4096	-0.20	***	-0.13	**	0.07	NS	-0.23	***	0.23	***	0.25	***	0.26	***
Edge8192	-0.32	***	-0.25	***	0.17	***	-0.28	***	0.27	***	0.27	***	0.27	***
Conn256	0.52	***	0.28	***	-0.30	***	0.37	***	-0.36	***	-0.35	***	-0.36	***
Conn512	0.35	***	0.19	***	-0.24	***	0.23	***	-0.25	***	-0.24	***	-0.24	***
Conn1024	0.28	***	0.15	**	-0.24	***	0.16	***	-0.17	***	-0.14	**	-0.15	**
Conn2048	0.30	***	0.07	NS	-0.15	**	0.13	**	-0.15	**	-0.11	**	-0.12	**
Conn4096	0.41	***	0.14	**	-0.24	***	0.18	***	-0.19	***	-0.15	**	-0.15	***
LDiv256	-0.32	***	-0.25	***	0.06	NS	-0.40	***	0.38	***	0.42	***	0.45	***
LDiv512	-0.31	***	-0.21	***	0.12	*	-0.36	***	0.35	***	0.38	***	0.41	***
LDiv1024	-0.39	***	-0.31	***	0.28	***	-0.45	***	0.44	***	0.45	***	0.49	***
LDiv2048	-0.45	***	-0.35	***	0.29	***	-0.45	***	0.43	***	0.44	***	0.46	***
LDiv4096	-0.59	***	-0.42	***	0.35	***	-0.53	***	0.51	***	0.52	***	0.54	***
LDiv8192	-0.49	***	-0.33	***	0.27	***	-0.42	***	0.41	***	0.41	***	0.42	***
Road256	0.17	***	0.00	NS	-0.04	NS	0.06	NS	-0.07	NS	-0.06	NS	-0.06	NS
Road512	-0.04	NS	-0.13	**	0.07	NS	-0.09	*	0.08	NS	0.09	NS	0.09	NS
Road1024	-0.10	*	-0.12	**	0.18	***	-0.14	**	0.18	***	0.16	***	0.15	**
Road2048	-0.60	***	-0.57	***	0.50	***	-0.60	***	0.58	***	0.57	***	0.59	***
Road4096	-0.62	***	-0.43	***	0.42	***	-0.49	***	0.47	***	0.45	***	0.46	***
Road8192	-0.18	***	-0.09	*	0.18	***	-0.05	NS	0.05	NS	0.02	NS	0.01	NS
Riv256	-0.25	***	-0.25	***	0.12	**	-0.23	***	0.19	***	0.20	***	0.19	***
Riv512	-0.47	***	-0.36	***	0.28	***	-0.34	***	0.31	***	0.30	***	0.29	***
Riv1024	-0.57	***	-0.44	***	0.29	***	-0.46	***	0.40	***	0.40	***	0.40	***
Riv2048	-0.61	***	-0.38	***	0.31	***	-0.43	***	0.40	***	0.38	***	0.38	***
Riv4096	-0.67	***	-0.38	***	0.29	***	-0.52	***	0.48	***	0.48	***	0.49	***
Riv8192	-0.76	***	-0.49	***	0.35	***	-0.60	***	0.55	***	0.55	***	0.56	***
Buil256	-0.15	***	-0.12	**	0.11	**	-0.12	**	0.11	*	0.09	*	0.10	*
Buil512	-0.35	***	-0.20	***	0.21	***	-0.18	***	0.17	***	0.14	**	0.14	**
Buil1024	-0.35	***	-0.26	***	0.30	***	-0.20	***	0.19	***	0.15	***	0.15	**
Buil2048	-0.44	***	-0.39	***	0.38	***	-0.33	***	0.30	***	0.28	***	0.27	***
Buil4096	-0.53	***	-0.37	***	0.36	***	-0.38	***	0.36	***	0.33	***	0.34	***
Buil8192	-0.58	***	-0.41	***	0.37	***	-0.44	***	0.41	***	0.39	***	0.40	***
NatF256	0.70	***	0.73	***	-0.57	***	0.69	***	-0.63	***	-0.63	***	-0.62	***
NatS256	0.03	NS	0.09	*	-0.04	NS	-0.01	NS	0.04	NS	0.05	NS	0.07	NS
ExoW256	-0.24	***	-0.09	*	0.04	NS	-0.13	**	0.11	*	0.10	*	0.11	*
ExoG256	-0.57	***	-0.68	***	0.55	***	-0.62	***	0.57	***	0.57	***	0.55	***
NatF512	0.76	***	0.75	***	-0.56	***	0.75	***	-0.69	***	-0.70	***	-0.70	***
NatS512	-0.02	NS	0.04	NS	0.00	NS	-0.06	NS	0.08	NS	0.09	NS	0.10	*
ExoW512	-0.24	***	-0.06	NS	0.04	NS	-0.13	**	0.11	*	0.10	*	0.12	**
ExoG512	-0.61	***	-0.70	***	0.51	***	-0.66	***	0.60	***	0.61	***	0.60	***
NatF1024	0.76	***	0.69	***	-0.52	***	0.74	***	-0.68	***	-0.70	***	-0.71	***
NatS1024	0.00	NS	0.01	NS	-0.01	NS	-0.07	NS	0.08	NS	0.09	NS	0.10	*
ExoW1024	-0.26	***	-0.15	***	0.09	*	-0.20	***	0.17	***	0.17	***	0.18	***
ExoG1024	-0.69	***	-0.66	***	0.47	***	-0.69	***	0.63	***	0.65	***	0.65	***
NatF2048	0.78	***	0.61	***	-0.51	***	0.71	***	-0.66	***	-0.66	***	-0.69	***
NatS2048	0.02	NS	0.02	NS	-0.03	NS	-0.07	NS	0.08	NS	0.09	*	0.11	*
ExoW2048	-0.40	***	-0.20	***	0.14	***	-0.28	***	0.25	***	0.25	***	0.27	***
ExoG2048	-0.70	***	-0.60	***	0.46	***	-0.69	***	0.64	***	0.65	***	0.67	***
NatF4096	0.82	***	0.64	***	-0.56	***	0.74	***	-0.70	***	-0.69	***	-0.71	***
NatS4096	0.52	***	0.40	***	-0.36	***	0.45	***	-0.44	***	-0.43	***	-0.45	***
ExoW4096	-0.47	***	-0.22	***	0.21	***	-0.33	***	0.32	***	0.31	***	0.33	***
ExoG4096	-0.76	***	-0.65	***	0.54	***	-0.74	***	0.70	***	0.71	***	0.73	***
NatF8192	0.63	***	0.47	***	-0.40	***	0.56	***	-0.53	***	-0.53	***	-0.54	***
NatS8192	0.37	***	0.32	***	-0.30	***	0.33	***	-0.31	***	-0.30	***	-0.30	***
ExoW8192	-0.38	***	-0.31	***	0.26	***	-0.37	***	0.36	***	0.37	***	0.37	***
ExoG8192	-0.67	***	-0.57	***	0.46	***	-0.63	***	0.60	***	0.60	***	0.62	***
256AX1	-0.14	**	-0.36	***	0.27	***	-0.25	***	0.22	***	0.23	***	0.21	***
256AX2	0.52	***	0.56	***	-0.40	***	0.53	***	-0.48	***	-0.48	***	-0.48	***
256AX3	0.28	***	0.35	***	-0.25	***	0.29	***	-0.24	***	-0.24	***	-0.23	***

256AX4	-0.31	***	-0.52	***	0.37	***	-0.40	***	0.36	***	0.36	***	0.34	***
512AX1	-0.10	*	-0.32	***	0.23	***	-0.23	***	0.20	***	0.22	***	0.21	***
512AX2	0.67	***	0.64	***	-0.48	***	0.63	***	-0.56	***	-0.56	***	-0.56	***
512AX3	0.04	NS	-0.07	*	0.00	NS	-0.02	NS	-0.01	NS	-0.01	NS	-0.02	NS
512AX4	0.70	***	0.66	***	-0.51	***	0.68	***	-0.62	***	-0.64	***	-0.64	***
1024AX1	-0.03	NS	-0.22	***	0.14	**	-0.15	**	0.13	**	0.14	**	0.14	**
1024AX2	0.65	***	0.53	***	-0.47	***	0.55	***	-0.51	***	-0.50	***	-0.51	***
1024AX3	-0.52	***	-0.51	***	0.37	***	-0.56	***	0.53	***	0.55	***	0.56	***
1024AX4	0.07	NS	-0.14	**	-0.02	NS	-0.05	NS	0.00	NS	0.02	NS	0.01	NS
2048AX1	-0.11	*	-0.27	***	0.17	***	-0.21	***	0.18	***	0.19	***	0.19	***
2048AX2	0.68	***	0.46	***	-0.46	***	0.49	***	-0.46	***	-0.43	***	-0.44	***
2048AX3	-0.38	***	-0.35	***	0.25	***	-0.47	***	0.45	***	0.48	***	0.50	***
2048AX4	0.72	***	0.46	***	-0.41	***	0.59	***	-0.56	***	-0.55	***	-0.58	***
4096AX1	-0.28	***	-0.40	***	0.29	***	-0.35	***	0.31	***	0.32	***	0.32	***
4096AX2	0.52	***	0.31	***	-0.34	***	0.34	***	-0.33	***	-0.30	***	-0.31	***
4096AX3	-0.59	***	-0.34	***	0.34	***	-0.43	***	0.41	***	0.39	***	0.41	***
4096AX4	-0.28	***	-0.27	***	0.19	***	-0.36	***	0.35	***	0.38	***	0.39	***
8192AX1	0.00	NS	-0.14	**	0.10	*	-0.05	NS	0.03	NS	0.03	NS	0.02	NS
8192AX2	0.58	***	0.40	***	-0.36	***	0.48	***	-0.46	***	-0.45	***	-0.47	***
8192AX3	0.18	***	0.25	***	-0.19	***	0.19	***	-0.16	***	-0.16	***	-0.15	**
8192AX4	0.49	***	0.47	***	-0.37	***	0.46	***	-0.42	***	-0.42	***	-0.42	***

Appendix 5

Formulae for logistic functions fitted to edge gradients in plant community composition at each fragment. Plant community composition is represented by Axis 1 scores from a partial detrended canonical correspondence analysis of plant species composition (<2 m in height).

Native forest cover in landscape	Fragment name	Fragment size class	Formula of logistic function for the edge response
19.8%	Maimai2	0.5-2 ha	y = 1.270+((-1.564-1.270)/(1+exp((0.038-X)*-0.597)))
	King6	2-8 ha	y = 0.927+((-0.985-0.927)/(1+exp((0.350-X)*-1.647)))
	Mawhera	8-32 ha	y = 1.037+((-1.056-1.037)/(1+exp((0.150-X)*-2.085)))
	Maimai	>32 ha	y =1.128+((-1.712-1.128)/(1+exp((0.516-X)*-0.669)))
25.5%	Blair2	0.5-2 ha	y =1.332+((-0.801-1.332)/(1+exp((0.204-X)*-0.590)))
	Blair6	2-8 ha	y =1.247+((-0.908-1.247)/(1+exp((-0.297-X)*-0.773)))
	Blair20	8-32 ha	y =0.899+((-0.922-0.899)/(1+exp((0.442-X)*-1.442)))
	Blair32	>32 ha	y =1.364+((-0.454-1.364)/(1+exp((0.583-X)*-1.133)))
26.7%	LittleB	0.5-2 ha	y =1.248+((-0.368-1.248)/(1+exp((0.063-X)*-2.168)))
	BerryP	2-8 ha	y =1.341+((-1.191-1.341)/(1+exp((-0.081-X)*-1.007)))
	BerryA	8-32 ha	could not fit logistic function
	Little	>32 ha	y = 1.118+((-1.806-1.118)/(1+exp((0.472-X)*-0.683)))
29.3%	Weka2	0.5-2 ha	y = 1.280+((-1.433-1.280)/(1+exp((0.193-X)*-1.148)))
	Weka6	2-8 ha	y = 0.792+((-2.848-0.792)/(1+exp((2.297-X)*-0.465)))
	Weka17	8-32 ha	y = 1.069+((-0.962-1.069)/(1+exp((0.839-X)*-0.812)))
	Weka97	>32 ha	y = 1.424+((-1.021-1.424)/(1+exp((0.339-X)*-0.809)))
30.6%	Ruru2	0.5-2 ha	y = 1.534+((-0.527-1.534)/(1+exp((-0.063-X)*-1.077)))
	Ruru4	2-8 ha	y = 1.306+((-0.544-1.306)/(1+exp((0.890-X)*-0.933)))
	Ruru10	8-32 ha	y = 0.946+((-2.372-0.946)/(1+exp((1.581-X)*-0.447)))
	Ruru126	>32 ha	y = 1.297+((-1.273-1.297)/(1+exp((0.188-X)*-0.646)))
31.5%	HahnC	0.5-2 ha	could not fit logistic function
	Savage	2-8 ha	y = 0.502+((-1.445-0.502)/(1+exp((0.166-X)*-2.997)))
	HahnB	8-32 ha	y = 1.160+((-1.599-1.160)/(1+exp((1.090-X)*-0.611)))
	Hahn32	>32 ha	y = 0.662+((-0.791-0.662)/(1+exp((0.436-X)*-1.599)))
31.8%	BellHill2	0.5-2 ha	y = 1.046+((-0.703-1.046)/(1+exp((0.040-X)*-1.276)))
	BellHill5	2-8 ha	y = 1.021+((-1.111-1.021)/(1+exp((0.580-X)*-0.785)))
	BellHill10	8-32 ha	could not fit logistic function
	BellHill112	>32 ha	y = 1.218+((-1.152-1.218)/(1+exp((-0.015-X)*-1.300)))
37.6%	McInroeC	0.5-2 ha	y = 1.063+((-0.968-1.063)/(1+exp((0.227-X)*-1.664)))
	McInroe	2-8 ha	y = 0.517+((-1.337-0.517)/(1+exp((0.274-X)*-2.859)))
	McInroeB	8-32 ha	y = 0.915+((-1.600-0.915)/(1+exp((0.114-X)*-1.508)))
	DOC62	>32 ha	y = 1.388+((-0.817-1.388)/(1+exp((-0.018-X)*-1.367)))
40.3%	Souters2	0.5-2 ha	y = 1.104+((-1.352-1.104)/(1+exp((-0.158-X)*-1.063)))
	Souters4	2-8 ha	y = 1.155+((-0.821-1.155)/(1+exp((0.406-X)*-1.336)))
	Souters23	8-32 ha	y = 0.906+((-0.908-0.906)/(1+exp((0.247-X)*-2.687)))
	Souters79	>32 ha	y = 1.181+((-0.960-1.181)/(1+exp((0.205-X)*-1.766)))
43.7%	Thompson09	0.5-2 ha	y = 0.853+((-1.567-0.853)/(1+exp((-0.033-X)*-1.553)))
	Thompson6	2-8 ha	y = 1.137+((-1.089-1.137)/(1+exp((0.220-X)*-1.103)))
	Somerville11	8-32 ha	y = 1.116+((-1.555-1.116)/(1+exp((0.055-X)*-0.822)))
	Somerville77	>32 ha	y = 0.899+((-1.296-0.899)/(1+exp((0.058-X)*-1.384)))
47.9%	FergusonC	0.5-2 ha	y = 1.479+((-1.018-1.479)/(1+exp((0.336-X)*-1.289)))
	Ferguson71	2-8 ha	y = 0.795+((-1.238-0.795)/(1+exp((0.297-X)*-0.813)))
	FergusonB	8-32 ha	y = 1.264+((-1.158-1.264)/(1+exp((-0.723-X)*-0.778)))
	DOC72	>32 ha	y = 1.023+((-0.917-1.023)/(1+exp((0.095-X)*-2.243)))

Appendix 6

Results from a partial canonical correspondence analysis (pCCA) of native plant species composition in all height tiers (i.e. cover scores as the species data). The sum of all unconstrained eigenvalues is after fitting 12 covariables (Landscape, Aspect, Altitude, and the spatial auto-correlation variables). Percentages are taken with respect to residual variances i.e. variances after fitting the covariables. A Monte Carlo test with 999 random permutations was used to test the significance of the first canonical axis and all canonical axes.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Total inertia**
Eigenvalues	0.149	0.086	0.066	0.060	3.218
Species-environment correlations	0.909	0.910	0.896	0.845	
Cumulative percentage variance					
of species data	5.9	9.2	11.8	14.2	
of species-environment relation	16.7	26.3	33.7	40.5	
Sum of all unconstrained eigenvalues					2.555
Sum of all canonical eigenvalues					0.895
					Significance of first canonical axis, $F = 15.598$, $p < 0.001$
					Significance of all canonical axes, $F = 4.364$, $p < 0.001$

Appendix 7

Pearson correlations (R^2) between the treatment variables – fragment area and distance from the forest edge – and the other environmental variables used in Chapter 5. Codes for environmental variables are given in **Chapter 5, Table 5.1**. Significance level: p <0.001***, p <0.01**, p <0.05*, NS = non-significant (p >0.05). N = 295.

Environmental variable	Fragment area (log_{10}, ha)		Distance from forest edge (m)	
	R^2	P	R^2	P
ShapeInd	0.753	<0.001***	-0.099	NS
Canopy	0.123	0.034*	-0.422	<0.001***
Grazing	-0.190	0.001**	0.108	NS
SoilpH	-0.053	NS	0.069	NS
SoilP	-0.005	NS	0.046	NS
SoilOM	-0.045	NS	-0.039	NS
SoilN	-0.138	0.017*	-0.025	NS
SoilCN	0.294	<0.001***	-0.058	NS
Drainage	0.173	0.003**	-0.054	NS
Tmin	0.026	NS	0.043	NS
Junes	0.037	NS	0.025	NS
Vpd	-0.068	NS	-0.001	NS
R2pet	0.146	0.012*	-0.009	NS
LENZ75	-0.106	NS	-0.007	NS
LENZ94	-0.081	NS	0.031	NS
LENZ96	-0.123	0.034*	0.022	NS
LENZ123	0.120	0.040*	-0.025	NS
LENZ150	0.058	NS	-0.003	NS
NND	0.232	<0.001***	-0.029	NS
NearBuil	0.122	0.036*	-0.036	NS
NearRoad	-0.038	NS	-0.020	NS
Road256	-0.082	NS	0.003	NS
Road512	-0.065	NS	0.008	NS
Road1024	0.012	NS	0.022	NS
Road2048	0.006	NS	0.005	NS
Road4096	0.018	NS	0.039	NS
Road8192	-0.033	NS	0.063	NS
Buil256	0.011	NS	0.012	NS
Buil512	-0.034	NS	0.017	NS
Buil1024	-0.108	NS	0.025	NS
Buil2048	-0.167	0.004**	0.043	NS
Buil4096	-0.016	NS	0.027	NS
Confounding variables				
Landscape	-0.044	NS	-0.049	NS
Aspect	-0.006	NS	0.040	NS
Altitude	0.090	NS	-0.047	NS

Appendix 8

Article follows

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Research Focus

Are invasive species the drivers of ecological change?

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Invasive species are widely accepted as one of the leading direct causes of biodiversity loss. However, much of the evidence for this contention is based on simple correlations between exotic dominance and native species decline in degraded systems. Although appealing, direct causality is not the only possible interpretation. A plausible alternative hypothesis is that exotic dominance could be the indirect consequence of habitat modification driving native species loss. In a new paper, MacDougall and Turkington now provide the first direct test of whether invasive species are the drivers of community change, or merely ‘passengers’ along for the environmental ride.